

THE GENERA OF EUPHORBIACEAE IN THE  
SOUTHEASTERN UNITED STATES<sup>1</sup>

GRADY L. WEBSTER

EUPHORBIACEAE A. L. de Jussieu, Gen. Pl. 384. 1789, "Euphorbiae"  
(SPURGE FAMILY)

Trees, shrubs, herbs, or vines; stems in some taxa succulent and often with colored or milky latex. Leaves alternate or opposite (or, rather rarely, whorled); stipules free or connate, or sometimes reduced to glandular bodies or absent; leaf blades pinnately or palmately veined, lobed, or compounded. Inflorescences basically cymose (dichasial), but often modified into apparent spikes, heads, or pseudanthia (or flowers sometimes solitary). Flowers unisexual (the plants monoecious or dioecious), basically regular; perianth showy to inconspicuous or absent, of valvate or quincuncially imbricate lobes or segments. Calyx deeply

<sup>1</sup>Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of George R. Cooley and the National Science Foundation and under the direction of Carroll E. Wood, Jr. This treatment follows the format established in the first paper in the series (Jour. Arnold Arb. 39: 296-346. 1958) and continued to the present paper. The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with supplementary information in brackets. References which the author has not seen are marked by an asterisk.

Part of the data recorded in this presentation have accrued from a long-term study of the reproductive morphology of the Euphorbiaceae which has been supported by several grants from the National Science Foundation (G-7148, G-18768, G-23604, GB-2801, GB-5669). I am especially indebted to Dr. Wood for his painstaking review of the manuscript and his many valuable suggestions. Special thanks are due to my wife, Barbara D. Webster, for her critical proofreading of the manuscript copy. Mrs. Gordon W. Dillon has helped greatly in checking the abbreviations for periodicals. Dr. Derek Burch supplied distributional information on certain taxa, and valuable collections of material were received from Mrs. Blanche Dean, Dr. Delzie Demaree, and Dr. John Thieret. The chromosome count of *Hippomane* was furnished through the courtesy of Dr. Jack Ellis. The illustrations were made by Arnold D. Clapman from dissections by Dr. Wood. These materials were collected for the *Generic Flora of the Southeastern United States* by Dr. Wood, Dr. F. C. Craighead, Dr. R. C. Rollins, Mr. Alan Strahler, and Dr. J. L. Thomas.

EDITOR'S NOTE. This treatment of the Euphorbiaceae, adhering to the plan of the *Flora* but much more extensive than the other papers published in this series and ranging over problems far beyond the geographical and taxonomic bounds of the *Generic Flora of the Southeastern United States*, is presented here in its entirety because of the unusual interest and difficulty of the Euphorbiaceae and the special relevance of this work to the taxonomic framework of the entire family.—C. E. WOOD, JR.

3-6-lobed or -parted in most taxa, but sometimes lobes more numerous, or reduced or absent. Corolla of mostly 3-6 separate or connivent petals (rarely more numerous or united), or often rudimentary or absent. Disc often present in flowers of one or both sexes, usually extrastaminal, of separate segments or cuplike. Stamens (1-)3-20[-400], inserted on a flat or convex receptacle; filaments free or united; anthers mostly 2-locular, dehiscing longitudinally; pollen tectate or intectate, inaperturate to polytreme (mostly tricolporate). Gynoecium of 3 or 4 united carpels [in the majority of taxa; reduced to 1 or multiplied up to 25 in others]; stigmas entire to bifid or lacerate; styles distinct to connate; ovary superior, 3- or 4-locular; placentation axile; ovules 1 or 2 per locule, anatropous or hemitropous, inserted beneath an obturator, crassinucellate, with 2 integuments, nucellus often prolonged as a beak in contact with the obturator. Fruit typically a capsular schizocarp, of 3 elastically dehiscent mericarps falling away from a persistent columella, but in some taxa drupaceous [baccate, or samaroid]. Seeds 1 or 2 per locule, or (by reduction) solitary in the fruit; seed coats thin to bony or fleshy; endosperm usually present; embryo straight or bent; cotyledons usually broader than the radicle, plane or (rarely) folded. Embryo sac normal, monosporic (*Polygonum* type) or in some disporic or tetrasporic. (Including Acalyphaceae Kl. & Garcke, Antidesmaceae Walp., Peraceae Kl. & Garcke, Phyllanthaceae Kl. & Garcke.) TYPE GENUS: *Euphorbia* L.

At once one of the largest and most diverse families of angiosperms, the Euphorbiaceae comprise some 7000 species in about 300 genera. Although the family is predominantly tropical, several hundred species of the tribe Euphorbieae, together with scattered species of primarily tropical genera such as *Croton*, are found in temperate regions. In the United States, 22 indigenous genera are known, 18 occurring in the southeastern United States. The 24 native and naturalized genera in the Southeast are represented by about 115 species.

The amplitude of morphological variation is so great that it is difficult to characterize the family, and, for this reason, many authors have suggested that it may be polyphyletic in origin. For the majority of genera, the family may be recognized by the unisexual flowers, the presence of a floral disc, and the trimerous gynoecium which typically ripens into a septicidally dehiscent schizocarp with three or six anatropous seeds. Vegetatively, the family is marked by having mostly alternate, stipulate leaves, often with glandular spots or appendages on the blades. Latex is present in many genera, but is far from being as ubiquitous as is implied by many textbooks.

The cymose inflorescences of many Euphorbiaceae are distinctly protogynous, the female flowers at the lower dichotomies of the inflorescence maturing before the males; this is especially clearly seen in *Jatropha*, *Cnidoscolus*, and many cyathia of *Euphorbia*. Pollination relationships have not been studied in the vast majority of genera, but the observations of Warmke on *Hevea* and the analysis of various floral characters suggest

that pollination of many tropical Euphorbiaceae is carried out mainly by small Diptera. Despite the frequent citation of the Euphorbiaceae as an example of a wind-pollinated family, only a few genera, such as *Acalypha* and *Ricinus*, seem to be truly anemophilous. Pollination by humming-birds has been observed in *Pedilanthus* and may occur in other red-bracteate taxa of tribe Euphorbieae.

Observations on weedy species of *Euphorbia* and *Phyllanthus* suggest that self-compatibility is widespread in many herbaceous Euphorbiaceae. Embryo sac development is of the normal, monosporic type in most genera, but tetrasporic types are prevalent in *Acalypha*, and, in *Euphorbia*, both bisporic and tetrasporic types have been recorded. Apomixis was long ago demonstrated by Strasburger in the Australian *Caelebogyne ilicifolia* J. E. Sm. which produces nucellar embryos (often with polyembryony). Adventitious embryony has also been found in *Euphorbia dulcis* L., but gametophytic apomixis has not been observed in the Euphorbiaceae.

Anatomical studies have shown that there is great variation in wood anatomy (particularly in fiber thickness, parenchyma distribution, and ray configuration), but no sufficiently comprehensive systematic survey of euphorbiaceous woods has yet been made. There is tremendous diversity in trichome shapes in some tribes (particularly the Crotonaeae), but very little in others (e.g., the Phyllanthaeae). Petiolar anatomy was studied by Dehay, whose conclusions as to family affinities seem excessively speculative; but within certain groups it may provide an excellent indication of affinity (e.g., in evaluating the supposed relationship of *Cnidoscolus* with *Jatropha*). The laticiferous organs of Euphorbiaceae have been studied intensively in such economically important genera as *Hevea* and *Manihot*, but still have not been surveyed in the manner necessary to obtain taxonomically significant data (cf. summation by Gaucher). Latex is not reported in any genus of the subfamily Phyllanthoideae, although *Bischofia* and *Uapaca* possess tanniniferous vessels which seem homologous with the "laticifers" of many Crotonoideae. The distinction between laticiferous and tanniniferous vessels is to some extent arbitrary, since the so-called laticifers in the Crotonoideae produce a great variety of compounds, including tannins, saponins, starch, resins, terpenoids, and rubber. Clearly, a study of the origin and evolution of the laticiferous systems in the Euphorbiaceae should throw a great deal of light on phylogenetic relationships within the family.

The Euphorbiaceae contain an extraordinary diversity of organic compounds, possibly more than in any other plant family. In addition to the compounds enumerated above, a variety of alkaloids has been found in both the Phyllanthoideae (especially subtribe Phyllanthinae) and Crotonoideae (mainly in *Croton*). The oily seeds of many Crotonoideae contain unusual fatty acids and also some peculiar, highly poisonous proteinaceous compounds (phytotoxins), the structures of which have not yet been elucidated. It seems clear that there is an exceedingly bright future for chemotaxonomic studies here.

Although there have been many studies on floral morphology in the Euphorbiaceae, few general surveys of the entire family have been made, other than those of Baillon and Michaelis. A disproportionate amount of effort has been expended on investigations of the cyathium of the Euphorbieae, but the results have, in many instances (e.g., Haber, Bodmann), been vitiated by the failure of authors to correlate meaningfully anatomical structure with the systematic position of the taxa studied. The use of floral characters as indicators of relationship has been complicated by the circumstance that trends of modification of floral parts have been both fluctuating and reversible. For example, the primitive euphorbiaceous flower was probably pentamerous with two whorls of stamens, to judge from morphological relationships among the primitive genera of Phyllanthoideae such as *Astrocasia*, *Heywoodia*, and *Wielandia*. During the evolution of other taxa, there has been a general overall trend towards reduction in number of parts, so that the gynoecium in the great majority of taxa is three-carpellate, and stamens are often reduced to five, or even to only one, per flower in the Euphorbieae and some Hippomaneae. On the other hand, a secondary increase in number has occurred in calyxlobes (e.g., up to 10 or 12 in *Dalechampia*), stamens (over 100 in several species of *Croton*), and carpels (10–20 in *Hura* and *Hippomane*).

One of the most fruitful subareas of floral morphology has been the investigation of pollen structure, which was started by Erdtman and further elaborated by Köhler, Punt, and Webster. Pollen characters seem, in many instances, to be extremely valuable indicators of affinity, as Erdtman originally suggested for the taxa with *Croton*-type pollen; Punt has shown that examination of the pollen makes possible an immediate and confident assignment of many genera to the proper tribe. The greatest diversity of pollen types is found within *Phyllanthus*, where the microspores may be tectate or intectate, prolate to oblate, inaperturate to tricolporate, polycolporate, pancolporate, or porate. The causes for this variation are still obscure, but it is notable that the gamut of pollen types in *Phyllanthus* rather strikingly parallels that in *Polygonum*, which has flowers of much the same size and configuration that probably are pollinated by similar agents (largely Diptera).

Ovule and seed characters are also important in the classification of the Euphorbiaceae but have not yet received the attention they deserve. Although the ovules are prevailingly anatropous, in the tribe Phyllanthaeae hemitropous ovules are common and seem to characterize natural groupings of genera. Plants such as *Tetracoccus*, with anatropous ovules which develop into shiny black seeds, clearly must be removed from the tribe. The seeds furnish important systematic characters at various levels of affinity, from characterizing species to separating tribes. Carunculate seeds are rare in the Phyllanthoideae but are quite common in the Crotonoideae, so much so that a number of uncritical writers have described the seeds of Euphorbiaceae as generally carunculate. In fact, however, the development of the caruncle is a very fluctuating character,

and within single genera (e.g., *Euphorbia*) rather closely related species may be separated by the presence or absence of the caruncle.

The schizocarpous fruit of Euphorbiaceae is generally described as a tricocous capsule, and the mericarps as cocci. There seems to be no reason to use these special names, since the fruit is essentially similar to that found in, for example, the Malvaceae. The elastic dehiscence of the fruit is characteristic, and seeds may be hurled to a considerable distance; those of *Hura* travel several yards, with a noise like a gun shot. Drupaceous fruits are found in a considerable number of Phyllanthoideae (many of these cauliflorous), and those of some tropical species of *Phyllanthus* are baccate. The carunculate seeds of various taxa are said to be dispersed by ants, but there is still insufficient field evidence to corroborate this.

Cytologically, the Euphorbiaceae are as diversified as in most other respects, but such a small proportion of the species (less than 5 per cent) has been studied that chromosome data are at present only of limited systematic usefulness. Except in some succulent species of *Euphorbia*, the chromosomes are relatively small, so cytological comparisons have to depend largely on number alone. Perry, who completed the first chromosomal survey of the family, concluded that the basic number is 8 and that annual species are more primitive than perennials. Subsequent studies, however, suggest that neither conclusion is justified. In the subfamily Phyllanthoideae it seems most likely that  $x=13$  in the more primitive taxa, while in the Crotonoideae the most widespread basic numbers are  $x=9$ , 10, and 11. Even in *Euphorbia* itself 10 seems more probable than 8 as the original basic number.

Polyploidy is frequent in many taxa, and taxonomically difficult polyploid complexes are known in *Mercurialis* and *Euphorbia* subg. ESULA. Translocation heterozygosity has been reported in *Croton californicus* Muell. Arg., and may be present in *Phyllanthus Niruri* L. Studies of interspecific hybridization have been made in weedy species of *Euphorbia* subg. ESULA, and such may prove interesting in *Croton* and other groups of *Euphorbia*; but on the whole, interspecific hybridization does not seem to be very conspicuous in the family.

The infrafamilial classification of the Euphorbiaceae has been a subject for controversy since Jussieu set up the first subfamilial divisions in 1824. Baillon initiated the primary division into one-ovulate and two-ovulate taxa which is still reflected in Pax's cleavage between Phyllanthoideae and Crotonoideae. Surprisingly, this division on the basis of a single character appears to be a relatively natural one, although the Crotonoideae are much more heterogeneous than are the Phyllanthoideae. Mueller (1866) established a different primary division, separating a relatively small group of Australian taxa as a "tribal series" Stenolobeae, characterized by narrow cotyledons (all other Euphorbiaceae falling into the series "Platylobeae" because of broader cotyledons). Mueller's two tribes of biovulate taxa and five tribes of uniovulate taxa were taken over by Pax, with some modification, as the basis of the system currently in general use.

Klotzsch and Garcke, writing contemporaneously with Baillon, initiated a policy of splitting the Euphorbiaceae which has been followed by a minority of workers; they recognized six families which were roughly the equivalents of Mueller's tribes. The most recent adherent of this philosophy is Hurusawa, who has promoted the four subfamilies of Pax (two of Stenolobeae and two of Platylobeae) to separate families. This procedure has little to recommend it, since the palynological evidence suggests that the Stenolobeae are probably an artificial group which should be returned to positions within the Platylobeae. Furthermore, while there is a rather sharp gulf between the uniovulate and biovulate Euphorbiaceae, they seem unquestionably to be related, and separation into different families overrates differences at the expense of similarities.

The proposal of Erdtman to realign the tribes of Crotonoideae on the basis of pollen morphology seems reasonable and is, on the whole, borne out by the detailed studies of Punt. As noted by Erdtman, this results in an arrangement much closer to that of Bentham than to that of any other of the 19th century systematists. Although no formal, revised system of the Crotonoideae has yet been published, it appears that many of the data necessary are already at hand.

Köhler's thorough analysis of pollen morphology in the biovulate Euphorbiaceae has, in general, confirmed and extended the observations of Erdtman and Punt. His rearrangement of the genera of Phyllanthoideae and absorption of the genera of the stenolobian Poranthoideae into their proper places among the platylobian genera represents a valuable contribution to the classification of the family. A few of his innovations (e.g., placing *Poranthera* in the Antidesmeae, rather than in the Andrachneae) do not accord with evidence from other data, but, on the whole, his new arrangement is undoubtedly much closer to the lines of natural affinity than any heretofore proposed.

The most interesting proposal of Köhler is to separate the mainly Old World biovulate genera with spinulose pollen grains as a separate subfamily. Because of the strong correlation with other morphological characters, this suggestion appears warranted, and the biovulate Euphorbiaceae are herewith assigned to two subfamilies: subfam. Phyllanthoideae Pax, with alternate leaves, nonspinulose pollen, ovules often hemitropous, and seeds not carunculate; and subfam. Oldfieldioideae Köhler & Webster,<sup>2</sup> with leaves often opposite or whorled, mostly spinulose pollen, ovules strictly anatropous, and seeds mostly carunculate.

<sup>2</sup> Köhler described several new suprageneric taxa which are invalidly published because he failed to provide Latin diagnoses. His proposed subfamily merits acceptance and is here validated: Subfam. **Oldfieldioideae** Köhler & Webster, subfam. nov. Arbores fruticesve saepe dioicae; foliis alternis, oppositis, verticillatisve, simplicibus vel palmatipartitis; floribus apetalis, disco plerumque nullo; staminibus liberis, granis pollinum echinulatis; ovulis in quoque loculo collateralibus. **TYPUS:** *Oldfieldia* Benth. et Hook. f.

Köhler's tribe Oldfieldieae was also invalidly published, but an earlier tribal name, Paivaeuseae, is validly published and available. As a consequence of Article 19 of the International Code of Botanical Nomenclature (1966), this virtually unpronounce-

By analogy with Köhler's proposal for the biovulate Euphorbiaceae, it might be possible to divide the uniovulate Euphorbiaceae (Crotonoideae and Ricinocarpoideae of Pax) into two subfamilies based on pollen morphology. Punt has shown convincingly that the genera with crotonoid pollen should be placed together in a single taxonomic grouping. However, the morphological and anatomical evidence does not show as good a correlation with palynological characters as is true for the biovulate Euphorbiaceae. For example, *Hevea* has articulated laticifers and in this and other respects seems related to *Manihot*; yet it has colpate pollen which lacks a distinct Croton-pattern. In terms of wood anatomy the uniovulate Euphorbiaceae are less diversified than the biovulate taxa, and there is no consistent difference in seed morphology. Tentatively, therefore, it seems preferable to retain all of the uniovulate Euphorbiaceae (including the stenolobian Ricinocarpoideae of Pax) in a single subfamily Crotonoideae.

The replacement of the subfamilial quartet of Pax by the present trinity does not make much difference in the classification of North American Euphorbiaceae, since the only genus of Oldfieldioideae represented is *Tetracoccus*. That small genus of xerophytic shrubs is confined to the western United States and Mexico and does not enter our area.

The extent of phylogenetic relationship between the Euphorbiaceae and other families has long been controversial. Baillon, in 1858, imagined a tetrahedral relationship, with the Euphorbiaceae on one face and the Malvales, Geraniales-Rutales, and Rhamnales on the other faces. Pax, summing up his studies in 1924, regarded the Euphorbiaceae as of polyphyletic (or at least diphyletic) origin, with part of their ancestors in the Geraniales-Sapindales complex, and part in the Malvales. Hutchinson, whose view is perhaps the most extreme, suggested an origin from at least four orders: Bixales, Tiliales, Malvales, Celastrales (and possibly also Sapindales). Croizat, in his principal consideration of the problem (1940), emphasized the affinity to the Malvales, especially the Sterculiaceae.

The existence of so many multifarious and disparate hypotheses suggests that little understanding of the problem of relationship at the family level has been achieved. Part of the confusion surrounding the affinities of the Euphorbiaceae resides in the unsatisfactory delimitation of the family. Taxa such as the Buxaceae, Dichapetalaceae, and Calitrichaceae were classified in the Euphorbiaceae by many 19th century authors, and families such as the Empetraceae were thought to be related until well into the 20th century. Until the Euphorbiaceae is purged of such aberrant groups, it will indeed be technically a "polyphyletic" family in the Hutchinsonian sense.

---

able name is automatically replaced by Oldfieldioideae when both subfamilies and tribes are used in the subfamilial classification. Although the result is the possibility of *two correct names* for the same taxon with precisely the same taxonomic circumscription and with no change in rank (an unfortunately unforeseen consequence of Article 19), it seems far preferable to describe a new subfamily based on *Oldfieldia* than to perpetrate a subfamilial name such as Paivaeusoideae!

While within the Euphorbiaceae the pollen grains furnish the most critical characters for delimitation of infrafamilial taxa, at the family level the ovules may be more significant. All bona fide Euphorbiaceae have pendent epitropous ovules, with the micropyle abaxial to the funicle and roofed over by an obturator. Such taxa as the Buxaceae, which have apotropous ovules, cannot be intimately related, and the derivation of the Euphorbiaceae from taxa within the apotropous Sapindales therefore appears unlikely. A relatively overlooked similarity exists between the Euphorbiaceae and the Simaroubaceae (*sensu lato*). In the Irvingioideae, often treated as a distinct family Irvingiaceae, gynoecia with epitropous ovules rather similar to those of the Euphorbiaceae occur. Recently, Capuron has described from Madagascar a new genus of Irvingiaceae, *Cleistanthopsis*, which, as its name indicates, has an extraordinary general similarity to *Cleistanthus*, of Euphorbiaceae subfam. Phyllanthoideae. Despite the solitary style and uniovulate locules, which preclude its being directly ancestral to the Ur-Euphorbiaceae, *Cleistanthopsis* obviously deserves consideration as at least a possible euphorbiaceous "great-uncle." Further botanical exploration in such regions as Madagascar may therefore eventually provide the solutions to some of the problems over which several generations of morphologists have quibbled in vain.

Part of the difficulty involved in tracing phylogeny within the Euphorbiaceae and in relating it to other families comes about because of the relatively poor fossil record. Kirchheimer (1957) disposed of most of the reports of fossil Euphorbiaceae from Central Europe; and in general, it would appear that records based on leaf impressions are even more unreliable than is usual in paleobotany, due to the large amplitude of foliar variation in Euphorbiaceae.<sup>3</sup> Recently, however, the picture has improved somewhat due to the discovery by Chandler of a considerable variety of fossil euphorbiaceous fruits from the Eocene of England, and the description of several fossil woods from India. The preservation of the English fruits and seeds is unexpectedly good, considering the dehiscent nature of the fruits and the thin seed-coats of most genera. The striking genus *Paleowetherellia* Chandl. has fruits which, in some respects, suggest the neotropical genus *Hura*, although the orientation of the ovules precludes identification with any known euphorbiaceous genus; it may possibly

<sup>3</sup> For a particularly egregious example of the ill-founded identifications perpetrated by some paleobotanists, see the paper by Potbury, who described a new species of the Old World genus *Microdesmis* from some leaves in a probably Eocene deposit in California. It would be difficult to find a genus of Euphorbiaceae with more unobtrusive leaves; those of *Microdesmis* could be matched by species in various other euphorbiaceous genera and in many other families such as Celastraceae, Flacourtiaceae, Theaceae, Moraceae, etc., etc. Her disposition can most charitably be characterized as a wild guess, and the fossils she referred to *Acalypha* and *Drypetes* are scarcely more convincing. Even the fossil leaves classified as *Aleurites* are only possibly congeneric. All of these remains could at best be ascribed to form-genera such as *Euphorbiophyllum*. Other Tertiary leaf fossils may be correctly ascribed to Old World genera (e.g., *Mallotus riparius*), but, to the writer's knowledge, there is as yet no unequivocal record of a living gerontogean euphorbiaceous taxon as a fossil in the New World, and vice versa.



represent some extinct branch of the family. Other carpic fossils are much closer to living taxa. For example, Chandler's *Euphorbiotheca lakensis*, which she compared to *Andrachne* and 'Securinega' (i.e., *Flueggea*), is a very close match for *Flueggea suffruticosa* (Pall.) Baill., a species widespread in Siberia and China and with a close relative in Japan.

Mädel, in a careful review of fossil euphorbiaceous woods, has shown that at least seven form-genera from the Cretaceous and Tertiary can be recognized. Unfortunately, the woods of many taxa of subfam. Phyllanthoideae are not very distinctive and can easily be confused with woods of other families, such as the Flacourtiaceae. Mädel rather convincingly compares her Upper Cretaceous *Paraphyllanthoxylon capense* with *Margaritaria discoidea* (Baill.) Webster,<sup>4</sup> a tree widespread in tropical Africa today. Bailey's *Paraphyllanthoxylon arizonense*, a roughly contemporaneous New World fossil, is less similar to the neotropical *Margaritaria nobilis* L. f., but may prove to be more similar to *Margaritaria* or *Phyllanthus* than to any other genera. There are now rather good records of Tertiary woods similar to those of living species of *Antidesma*, *Bridelia*, *Aleurites*, and *Hevea*. If these fossil woods can be matched with fossils of fruits and seeds (as found in the English deposits), there would appear to be a good opportunity to make much more nearly definitive identifications and thus to produce — at last — some historical documentation to prop up the rather shaky phylogenetic classification of the family.

A number of botanists over the past century have sought to resolve some of the problems of the phylogenetic position of Euphorbiaceae by excluding various extraneous elements. Baillon proposed the removal of the Buxaceae and was followed in this by Mueller, though not by Bentham. Today it appears that the resemblance of Buxaceae to Euphorbiaceae is superficial, as the boxwoods differ in a number of fundamental characters. The perianth of the Buxaceae does not appear to be strictly homologous with that of Euphorbiaceae, as it consists of four decussate tepals in the male flower and about six to twelve imbricate bractlike tepals in the female flower. The gynoecium of Buxaceae is very different in having the styles emerging laterally, not apically, on the ovary, as well as in the apotropous ovules; and at least in *Buxus* and *Pachysandra*, endosperm development is cellular, rather than nuclear. Despite the tantalizing similarity between the pollen grains of *Buxus* and *Pachysandra* with those of various Euphorbiaceae (subfam. Crotonoideae), it appears most probable that this resemblance is due to convergence and is not indicative of affinity.

Somewhat more similar to the Euphorbiaceae is the genus *Daphniphyllum*, which resembles some taxa of subfam. Phyllanthoideae in both habit and its gynoecium with paired, anatropous, epitropous ovules. However, *Daphniphyllum* diverges markedly in its exstipulate leaves, imperfectly septate ovary, ovules without an obturator, and especially in its seeds

<sup>4</sup> *Margaritaria discoidea* (Baill.) Webster, comb. nov. *Cicca discoidea* Baill. *Adansonia* 1: 85. 1860. *Phyllanthus discoideus* (Baill.) Muell. Arg. *Linnaea* 32: 51. 1863.

with a minute embryo. The latter feature suggests Ranalian affinities for *Daphniphyllum* and makes it necessary to exclude it from the Euphorbiaceae as the only genus of a separate family Daphniphyllaceae. The wood of *Daphniphyllum*, according to Janssonius, is very different from any Euphorbiaceae and resembles that of Hammamelidaceae, thus confirming the suggestion of affinity made by Hallier. In its gynoeceal conformation, *Daphniphyllum* shows some resemblance to the Buxaceae despite its differently oriented ovules; and it also resembles *Buxus* in its exstipulate leaves and cellular endosperm. It would appear, therefore, that the Daphniphyllaceae are at least much more closely related to the Buxaceae than either family is to the Euphorbiaceae; and both probably belong in the Hammamelidales-Trochodendrales complex, but with their exact positions yet to be determined.

Still other genera which have been viewed with suspicion as to their euphorbiaceous parentage include *Aextoxicon*, *Bischofia*, and *Picrodendron*. *Aextoxicon*, which somewhat resembles the euphorbiaceous genus *Pera* in habit (partly because of its lepidote indumentum), has been excluded from the Euphorbiaceae by Pax on the basis of its aberrant perianth, apotropous ovules, and ruminant endosperm. As the only representative of the family Aextoxicaceae, it would according to Pax take a position adjacent to the Icacinaceae. *Picrodendron*, a West Indian genus with compound leaves and fruits superficially like walnuts, has been variously placed in the Simaroubaceae, Euphorbiaceae, or in its own family, Picrodendraceae. The female flower of *Picrodendron* (illustrated by Fawcett and Rendle) is quite typical for the Euphorbiaceae, as the anatropous ovules are inserted below an obturator. The genus therefore may be truly euphorbiaceous, and its leaves and spinulose pollen suggest a possible affinity with genera of the subfamily Oldfieldioideae.

*Bischofia* presents a more difficult problem. Although the genus resembles some of the subfam. Oldfieldioideae in habit, the pollen is different, and the wood structure is not readily distinguishable from that of some taxa of subfam. Phyllanthoideae. Airy Shaw has proposed to create a separate family Bischofiaceae, to be placed near Staphyleaceae because of the resemblance between *Bischofia* and the Chinese genus *Tapiscia*. *Bischofia* differs from *Tapiscia* in so many ways (e.g., unisexual flowers, nearly free calyx segments, completely different gynoeceum, and larger embryo) that a very close relationship between the two genera can scarcely be maintained. Nevertheless, *Bischofia* is so isolated in the Euphorbiaceae that its exclusion is quite possibly warranted, and Airy Shaw's suggestion of a staphyleaceous kinship deserves further investigation.

Airy Shaw has also created new unigeneric families for *Androstachys*, *Hymenocardia*, and *Uapaca*; but, although each of these taxa is certainly aberrant, they have the fundamental gynoeceal characters of Euphorbiaceae, and there does not seem to be any compelling reason why they should be removed.

A rather surprising realignment of the boundaries of the Euphorbiaceae

has recently been proposed by Forman, who has removed *Microdesmis* and *Galearia* to the family Pandaceae, which heretofore included only the anomalous African genus *Panda*. Forman's arguments for an affinity between the three genera seem convincing, and it must be noted that *Microdesmis* and *Galearia* have always occupied a rather anomalous position in the Euphorbiaceae; Bentham created a special tribe Galearieae, apparently because he could not place them with any other group of genera. *Microdesmis* is aberrant from most other Euphorbiaceae in its basic chromosome number of  $x=15$ , in the compression of the anthers against the vestigial gynoecium or petals in the male flower bud, and in the absence of an obturator. *Galearia* shares at least some of these characters, and both genera have a wood structure unlike that of other uniovulate Euphorbiaceae. Although it is difficult to write a diagnosis for the revised family Pandaceae which will unequivocally exclude all Euphorbiaceae, the inclusion of *Panda* — with its orthotropous ovules and unusual fruit — would make the Euphorbiaceae more difficult to circumscribe. Consequently, it seems expedient to recognize the Pandaceae as an offshoot of the Euphorbiaceae and the only other family which is at all closely allied.

When the Buxaceae, Daphniphyllaceae, and Pandaceae are excluded, the question remains as to where the closest affinities of the Euphorbiaceae are to be found. Despite all the additional information which has accrued, it must be admitted that no single taxon ancestral to the Euphorbiaceae can be designated at the present time, and it is not certain that any living taxon will ever be identified as the progenitor. The relationships of the polypetalous woody dicotyledons are notoriously reticulate, and the best that can be done at present is to specify the most plausible phylogenetic groupings. The inclusion of the Euphorbiaceae within the Geraniales of Engler appears to be justified, since in wood anatomy, floral morphology, and ovule and seed structure they resemble such families as Linaceae, Oxalidaceae, and Irvingiaceae. On the other hand, with respect to certain characters there are undeniable similarities to other groups, especially the Sterculiaceae and Thymelaeaceae, which show some striking similarities in pollen and seed structure. Croizat, among others, has emphasized the sterculiaceus affinity, but it should be noted that most of the malvalian-appearing Euphorbiaceae belong to the Crotonoideae, and the presumably more primitive Phyllanthoideae show little resemblance. Perhaps the similarities of Euphorbiaceae with the malvlean families and with the Flacourtiaceae may be explained as parallelism, in the sense that all of these families represent divergent branches of a plexus that may ultimately be of rosalian origin. It is not possible to go any further than that on the basis of current botanical knowledge.

Because of their chemical diversity, the Euphorbiaceae include a rather large number of plants of economic importance. Although rubber from *Hevea* is perhaps the most valuable commodity, commercially important products are also obtained from euphorbiaceous seed oils (*Aleurites*, *Ricinus*, and, to a lesser extent, *Croton* and *Jatropha*), starchy tubers (*Manihot*), and waxes (*Aleurites*, *Sapium*, and *Euphorbia*). Still other

compounds, such as the alkaloids and saponins in the Phyllanthoideae, may yet prove to be of medicinal value. Finally, a number of Euphorbiaceae are grown as ornamentals. The most important species is doubtless the poinsettia (*Euphorbia pulcherrima* Willd. ex Grah.), but especially in tropical and subtropical gardens one may encounter species of *Phyllanthus*, *Acalypha*, *Croton*, *Codiaeum* (the widely cultivated "Croton" of horticulturalists), *Euphorbia*, and *Pedilanthus*.

In addition to the 24 genera treated in detail below, some of these ornamental or economically important plants may be found cultivated in our area, especially in southern Florida. The Pará rubber tree, *Hevea brasiliensis* (Willd. ex A. Juss.) Muell. Arg., may be found in Key West and perhaps extreme southern Florida; it can be recognized by its long-petiolate trifoliolate leaves, paniculate inflorescences, apetalous flowers, and large fruits. Another euphorbiaceous tree planted in the Miami area, *Bischofia javanica* Blume, also has trifoliolate leaves but the leaflets are toothed (instead of entire as in *Hevea*) and the twigs produce no latex. Various species of *Antidesma* are cultivated, especially *A. Bunius* (L.) Spreng.; these are easily distinguished from other Euphorbiaceae by the combination of entire laurel-like leaves and the spicate female flowers which mature into edible drupaceous fruits. One of the most characteristic trees which may be seen in the Miami area is the sandbox tree, *Hura crepitans* L., immediately recognizable by virtue of its spiny stem, laticiferous twigs, heart-shaped leaves, bizarre flowers (the female with a dilated umbrella-like stigma), and large multicarpellate fruits which dehisce in a violent explosion. The latex and the seeds of this plant, as in many other local Euphorbiaceae of subfam. Crotonoideae, are dangerously poisonous, and plantings close to houses should be made with care.

#### REFERENCES:

- AIRY SHAW, H. K. Notes on Malaysian Euphorbiaceae. I. Kew Bull. 3: 484. 1949; II–XV. *Ibid.* 14: 353–397. 1960; XVI–XIX. *Ibid.* 469–479.
- . Notes on Malaysian and other Asiatic Euphorbiaceae. XX–XLVIII. *Ibid.* 16: 341–372. 1963; XLIX–LV. *Ibid.* 19: 299–328. 1965; LVI–LXVI. *Ibid.* 20: 25–49. 1966; LXVII–LXXXII. *Ibid.* 379–415. [Many new spp. and several new genera described in this series.]
- . Diagnoses of new families, new names, etc., for the seventh edition of Willis's "Dictionary". *Ibid.* 18: 249–273. 1965. [Describes 4 new families: Androstachyaceae, Bischofiaceae, Hymenocardiaceae, and Uapacaceae.]
- ARNOLDI, W. Zur Embryologie einiger Euphorbiaceen. Trav. Mus. Bot. Acad. Sci. St.-Pétersb. 9: 136–154. 1912. [Gives some details of megasporogenesis in 2 spp. of *Phyllanthus* and individual spp. of *Acalypha*, *Codiaeum*, *Glochidion*, *Jatropha*, *Pedilanthus*, and *Trigonostemon*.]
- ASSAILLY, A. Contribution à la détermination des Euphorbiacées par la méthode anatomique. Bull. Soc. Hist. Nat. Toulouse 89: 157–194. 1954. [Deals largely with cultivated or medicinal spp. of France.]
- BAILEY, I. W. The problem of identifying the wood of Cretaceous and later Dicotyledons: *Paraphyllanthoxylon arizonense*. Ann. Bot. 38: 439–451. pl. 15. 1924.

- BAILLON, H. Anthostemidearum sive Euphorbiacearum monandrarum descriptionem. *Ann. Sci. Nat. Bot.* IV. 9: 192-204. 1858.
- . Étude générale du groupe des Euphorbiacées. 684 pp. 27 pls. Paris. 1858.
- . Species Euphorbiacearum. A. Euphorbiacées Africaines. *Adansonia* 1: 58-87. 1860; 139-173, 251-286. *pl.* 5. 1861; 2: 27-55. 1861; 3: 133-166. 1863 (?).
- . Énumération des Euphorbiacées cultivées dans les Jardins Botaniques de Paris. *Ibid.* 1: 104-117. 1860; 340-352. 1861.
- . Species Euphorbiacearum. Euphorbiaceae Neo-Caledonicae. *Ibid.* 2: 211-242. 1862.
- . Species Euphorbiacearum. Euphorbiacées Americaines. *Ibid.* 4: 257-377. 1864; 5: 221-240, 305-360. 1865.
- . Species Euphorbiacearum. Euphorbiacées Australiennes. *Ibid.* 6: 282-345. 1866.
- . Sur la parthénogénèse et la suppression du genre *Caelebogyne*. *Ibid.* 368-379.
- . Nouvelles observations sur les Euphorbiacées. *Ibid.* 11: 72-138. *pl.* 9. 1873. [Interesting discussion of Baillon's philosophy of classification in the Euphorbiaceae, including a defense of his extremely broad circumscriptions of such genera as *Antidesma*, *Phyllanthus*, *Tournefortia*, and *Excoecaria*.]
- . Euphorbiacées. *Hist. Pl.* 5: 105-256. 1874.
- BANERJI, I., & M. K. DUTT. The development of the female gametophyte in some members of the Euphorbiaceae. *Proc. Indian Acad. Sci. B.* 20: 51-60. 1944. [*Putranjiva*, *Trewia*, *Phyllanthus*, *Chamaesyce*.]
- BENTHAM, G. Notes on Euphorbiaceae. *Jour. Linn. Soc. Bot.* 17: 185-267. 1878.
- & J. D. HOOKER. Euphorbiaceae. *Gen. Pl.* 3: 239-340. 1880. [Treatment prepared by Bentham.]
- BLOHM, H. Poisonous plants of Venezuela. xvi + 136 pp. Cambridge, Mass. 1962. [Euphorbiaceae, 47-61.]
- BRAUN, A. Über Polyembryonie und Keimung von *Caelebogyne*. *Abh. Akad. Wiss. Berlin* 1859: 109-263. *pls.* 1-6. 1860. [Discussion of *Caelebogyne* mainly on pp. 109-131.]
- BROWN, N. E., J. HUTCHINSON, & D. PRAIN. Euphorbiaceae. *In*: W. T. THISELTON-DYER, ed., *Fl. Trop. Afr.* 6(1): 441-1020, 1034-1059. 1911-1913. [Pp. 441-576. 1911; pp. 577-960. 1912; pp. 961-1059. 1913.]
- . Euphorbiaceae. *In*: W. T. THISELTON-DYER, ed., *Fl. Capensis* 5(2): 216-516, 585, 586. 1915-1925. [Pp. 216-384. 1915; pp. 385-516. 1920; pp. 585, 586. 1925.]
- BROWN, W. H. The bearing of nectaries on the phylogeny of flowering plants. *Proc. Am. Philos. Soc.* 79: 549-595. *pls.* 1-12. 1938.
- CAPURON, R. Une Irvingiacée Malgache. *Adansonia* II. 5: 213-216. 1965. [*Cleistanthopsis multicaulis* Cap., gen. & sp. nov.; similar in habit and some reproductive characters to Euphorbiaceae subfam. Phyllanthoideae.]
- CHANDLER, M. J. Some Upper Cretaceous and Eocene fruits from Egypt. *Bull. Brit. Mus. Geol.* 2: 147-187. *pls.* 10-16. 1954. [Presumed Euphorbiaceae, *Lagenoidea* and new genus *Palaeowetherellia*, 166-178.]
- COCKERELL, T. D. A. Fossil Euphorbiaceae, with a note on Saururaceae. *Torreyana* 9: 117-119. 1909.

- CROIZAT, L. Glands of Euphorbiaceae and of *Euphorbia*. Chron. Bot. 4: 512-514. 1938.
- . On the phylogeny of the Euphorbiaceae and some of their presumed allies. Revista Univ. Chile 25: 205-220. 1940.
- . Notes on the Euphorbiaceae. II. Bull. Bot. Gard. Buitenzorg III. 17: 204-208. 1941.
- . Peculiarities of the inflorescence in the Euphorbiaceae. Bot. Gaz. 103: 771-779. 1942a.
- . New and critical Euphorbiaceae chiefly from the southeastern United States. Bull. Torrey Bot. Club 69: 445-460. 1942b. [Notes on *Croton*, *Manihot*, and *Tetracoccus*, including new spp. & combs.]
- . Notes on American Euphorbiaceae, with descriptions of eleven new species. Jour. Wash. Acad. Sci. 33: 11-20. 1943a.
- . Novelties in American Euphorbiaceae. Jour. Arnold Arb. 34: 165-189. 1943b.
- . Bibliographical notes on the Euphorbiaceae. Revista Acad. Colomb. Ci. Exact. Fis. Nat. 5: 541-547. 1944. [A valuable but not readily available review of exact dates of publications by Baillon, Mueller, and Klotzsch.]
- . Novelties in American Euphorbiaceae. Jour. Arnold Arb. 27: 289-291. 1946.
- DE WILDEMAN, E. Les latex des Euphorbiacées. I. Considérations générales. Mém. Inst. Colon. Belge Sci. Nat. Med. Collect. 8° 12(4): 1-68. 1944.
- DÄNIKER, A. U. Über die Euphorbiaceen und die Entwicklung der Monochlamydeae. Arch. Julius Klaus-Stiftung 21: 465-469. 1945. [An effort to find relationships between Euphorbiaceae, Balanopaceae, and Juglandaceae.]
- DEHAY, C. L'appareil libero-ligneux foliaire des Euphorbiacées. Ann. Sci. Nat. Bot. X. 17: 147-290. pls. 1-4. 1935.
- DELPINO, F. Applicazione di nuovi criterii per la classificazione delle piante. Terza memoria. Mem. Accad. Sci. Ist. Bologna IV. 10: 565-599. 1 pl. 1889. [Pseudanthia in Euphorbiaceae, 572-580.]
- EICHLER, A. W. Blüthendiagramme construiert und erläutert. vol. 2. xx + 575 pp. Leipzig. 1878. [Euphorbiaceae, 385-398; Euphorbieae treated in considerable detail.]
- ERDTMAN, G. Pollen morphology and plant taxonomy. Angiosperms. xii + 539 pp. Stockholm; Waltham, Mass. 1952. [Euphorbiaceae, 165-175.]
- FORMAN, L. L. The reinstatement of *Galearia* Zoll. & Mor. and *Microdesmis* Hook. f. in the Pandaceae. Kew Bull. 20: 309-321. pl. 5. 1966. [Includes appendices on leaf and stem anatomy by C. R. METCALFE and on wood structure by N. PARAMESWARAN & METCALFE.]
- FROEMLING, W. Anatomisch-systematische Untersuchung von Blatt und Axe der Crotoneen und Euphyllantheen. 76 pp. 2 pls. Inaug.-diss. Cassel. 1896.
- GAGNEPAIN, F., & L. BEILLE. Euphorbiacées. Fl. Gén. Indo-Chine 5(4): 229-372. 1925; 5(5): 373-516. 1926; 5(6): 517-673. 1927. [Phyllanthae by BEILLE; remainder by GAGNEPAIN.]
- GAUCHER, L. Recherches anatomiques sur les Euphorbiacées. Ann. Sci. Nat. Bot. VIII. 15: 161-309. 1902.
- GIBBS, R. D., J. T. EDWARD, & J. M. FERLAND. A novel colour reaction of some *Euphorbia* and *Oxyanthus* species. Phytochemistry 6: 253-257. 1967. [Orange color reaction to 2.5 per cent HCl in methanol shown by 3 spp. of *Euphorbia*, and by certain other Euphorbiaceae, especially Phyllanthoideae.]
- GRISEBACH, A. Erläuterungen augeswählter Pflanzen des tropischen Amerikas.

- Abh. Ges. Wiss. Göttingen 9: 3-58. 1861. [Euphorbiaceae, including a subfamilial classification, 11-21.]
- GRÜNING, G. Euphorbiaceae-Porantheroideae et Ricinocarpoideae. Pflanzenreich IV. 147(Heft 58): 1-97. 1913.
- HANSGIRG, A. Ueber die phyllobiologischen Typen einiger Fagaceen, Monimiaceen, Melastomaceen, Euphorbiaceen, Piperaceen und Chloranthaceen. Beih. Bot. Centralbl. 10: 458-480. 1901. [Euphorbiaceae, 472-479.]
- HEGENAUER, R. Chemotaxonomie der Pflanzen. Band 4. Dicotyledoneae: Daphniphyllaceae-Lythraceae. 551 pp. Basel & Stuttgart. 1966. [Euphorbiaceae, 103-140, 490-492; a valuable compendium of information with extensive references, examined too late for much of the appropriate information to be incorporated into this paper.]
- HERBERT, H. Anatomische Untersuchung von Blatt und Axe der Hippomaneen. Inaug.-diss. 62 pp. Munich. 1897.
- HURUSAWA, I. Eine nochmalige Durchsicht des herkömmlichen Systems der Euphorbiaceen im weiteren Sinne. Jour. Fac. Sci. Univ. Tokyo Bot. 6: 209-342. pls. 1-4. 1954.
- INGRAM, J. Notes on the cultivated Euphorbiaceae. 1. The flowers of the Euphorbiaceae. 2. *Cnidioscolus* and *Jatropha*. Baileya 5: 107-117. 1957.
- JABLONSKY, E. Euphorbiaceae-Phyllanthoideae-Brideliaceae. Pflanzenreich IV. 147-VIII(Heft 65): 1-98. 1915.
- . Notes on neotropical Euphorbiaceae. 1. Synopsis of South American *Sapium*. Phytologia 14: 441-449. 1967. [Includes key to 58 spp. recognized, generalized map.] 2. New species and transfers. *Ibid.* 450-456. pls. 2-4. [All in the Hippomaneae.]
- JANSSONIUS, H. H. Mikrographie des Holzes der auf Java vorkommenden Baumarten. Vol. 5. Monochlamydeae I. 835 pp. Leiden. 1934. [Euphorbiaceae, 442-812; perhaps the most critical study of wood anatomy done in the family.]
- . Wood anatomy and relationship. Blumea 6: 407-461. 1950. [Note 2, possible relationship of Euphorbiaceae with various other families, 414-416.]
- JUSSIEU, A. DE. Considerations sur la famille des Euphorbiacées. Mém. Mus. Hist. Nat. Paris 10: 317-355. 1823.
- . De Euphorbiacearum generibus medicisque earumdem viribus tentamen. 118 pp. pls. 1-18. Paris. 1824.
- KINGSBURY, J. M. Poisonous plants of the United States and Canada. xiii + 626 pp. Englewood Cliffs, New Jersey. 1964. [Euphorbiaceae, 182-197; extensive bibliographic references.]
- KIRCHHEIMER, F. Die Laubgewächse der Braunkohlenzeit. ix + 783 pp. Halle a.d. Saale. 1957.
- KLOTZSCH, F. Linne's natürliche Pflanzenklasse *Tricoccae* des Berliner Herbarium's in Allgemeinen und die natürliche Ordnung Euphorbiaceae insbesondere. Monatsber. Akad. Wiss. Berlin 1859: 236-254. 1859; Abh. Akad. Wiss. Berlin 1859: 1-108. 1860. [Pp. 1-19 essentially duplicating the 1859 publication.]
- KÖHLER, E. Die Pollenmorphologie der biovulaten Euphorbiaceae und ihre Bedeutung für die Taxonomie. Grana Palynol. 6: 26-120. pls. 1-9. 1965. [Proposes new subfam. & tribe based on *Oldfieldia*; no Latin descriptions.]
- LAKELA, O., & F. C. CRAIGHEAD. Annotated checklist of the vascular plants of Collier, Dade, and Monroe counties, Florida. 95 pp. Fairchild Trop. Gard. & Univ. Miami Press, Coral Gables. 1965. [Euphorbiaceae, 52-55.]

- LANJOUW, J. The Euphorbiaceae of Surinam. 195 pp. *pls.* 1-5. 1 *fold. map.* Amsterdam. 1931.
- LEANDRI, J. Sur la distribution et les affinités des Phyllanthées de Madagascar. *Bull. Soc. Bot. France* 84: 61-72, 93-98. 1937.
- . Notes systématiques sur les Euphorbiacées-Phyllanthées de Madagascar. *Mém. Inst. Sci. Madagascar B.* 8: 205-261. 1957. [Descriptions of a number of primitive Phyllanthoideae, including *Blotia*, gen. nov.]
- . Euphorbiacées. *In*: H. HUMBERT, *Fl. Madagascar Comores* 111<sup>e</sup> Fam. 1-209. Paris. 1958. [Subfam. Phyllanthoideae only.]
- LÉONARD, J. Euphorbiaceae [part 1]. *Fl. Congo* 8(1): 1-214. *pls.* 1-13. 1962. [Includes tribes Brideliaceae, Crotonaceae, Clusiaceae, Geloniaceae, Hippomaniaceae, Chrozophoreae, and Dalechampiaceae; excellent descriptions and illustrations.]
- LONGWOOD, F. R. Present and potential commercial timbers of the Caribbean. *U. S. Dep. Agr. Agr. Handb.* 207: 1-167. 1962. [Includes discussions of wood of *Drypetes* and *Hura*.]
- LOURTEIG, A., & C. A. O'DONELL. Acalypheae Argentinae (Euphorbiaceae). *Lilloa* 8: 273-333. *pls.* 1-9. 1942. Euphorbiaceae Argentinae. Phyllanthaceae, Dalechampiaceae, Clusiaceae, Manihoteae. *Ibid.* 9: 77-173. *pls.* 1-18. 1943.
- LUNDBERG, F. Bemerkungen über die Embryosackentwicklung bei *Codiaeum*. *Bot. Not.* 1931: 346-349. 1931. [Demonstrates Polygonum-type development, contrary to an earlier report.]
- LUNDELL, C. L. The genus *Garcia* Vahl, a potential source of superior, hard, quick-drying oil. *Wrightia* 1: 1-12. 1945. [Reports *G. nutans* native to e. Mexico & describes *G. parviflora* from Tabasco.]
- McVAUGH, R. Euphorbiaceae novae novo-galicianaee. *Brittonia* 13: 145-205. *map.* 1961. [Includes new spp. in *Acalypha*, *Bernardia*, *Croton*, *Euphorbia*, *Manihot*, *Phyllanthus*, *Sebastiania*, and *Tragia*.]
- MÄDEL, E. Die fossilen Euphorbiaceen-Hölzer mit besonderer Berücksichtigung neuer Funde aus der Oberkreide Süd-Afrikas. *Senckenberg. Lethaea* 43: 283-321. *pls.* 34-38. 1962. [Critical revision with descriptions of new gen. *Securinegoxylon* and *Aleuritoxylon*.]
- MANDEL, K. Beitrag zur Kenntnis der Anatomie der Samen mehrerer Euphorbiaceen-Arten. *Österr. Bot. Zeitschr.* 75: 1-17. *pls.* 1-4. 1926.
- MANGENOT, G. Sur le mode de formation des graines d'amidon dans les laticifères des Euphorbiacées. *Compt. Rend. Acad. Sci. Paris* 180: 157-160. 1925.
- MARTICORENA, C. Morfología de los granos de polen de Euphorbiaceae chilenas. *Gayana Bot.* 5: 3-12. 1962. [Describes pollen of spp. of *Croton*, *Chiro-petalum*, *Colliguaya*, *Avellanita*, *Adenopeltis*, and *Dysopsis*.]
- MATTEI, G. E. Frammenti de morfologia florale I. Euforbiacee. *Malpighia* 22: 475-498. *pl.* 2. 1908.
- METCALFE, C. R., & L. CHALK. Anatomy of the dicotyledons. Vol. II. pp. 725-1500. Oxford. 1950. [Euphorbiaceae, 1207-1235; includes a systematic arrangement of taxa according to wood structure.]
- MICHAELIS, P. Blütenmorphologische Untersuchungen an den Euphorbiaceen. *Bot. Abh. Jena* 3: 1-150. *pls.* 1-41. 1924.
- MILANEZ, F. R. Nota prévia sôbre os laticíferos de *Hevea brasiliensis*. *Arq. Serv. Florestal Rio Janeiro* 2: 39-65. 1946.
- . Segunda nota sôbre os laticíferos. *Lilloa* 16: 193-211. 1949.
- MILLER, K. I., & G. L. WEBSTER. Chromosome numbers in Euphorbiaceae. *Brittonia* 18: 372-379. 1967 ("1966").
- MODILEWSKI, J. Weitere Beiträge zur Embryobildung einiger Euphorbiaceen.



- Ber. Deutsch. Bot. Ges. 28: 413-418. *pl.* 12. 1910. [Reports on several spp. of *Euphorbia* plus single spp. of *Croton*, *Phyllanthus*, *Ricinus*, and *Securinega*.]
- MONTANT, C. Modifications de la phyllotaxie observées sur quelques Euphorbiacées parasitées. Compt. Rend. Soc. Biol. 151: 1431-1434. 1957. [Parasitized by *Uromyces* and *Endophyllum*.]
- MUELLER, J. Euphorbiaceae. Vorläufige Mitteilungen aus dem für De Candolle's Prodr. bestimmten Manuscript. Linnaea 32: 1-126. 1863; 34: 1-224. 1865.
- . Neue Euphorbiaceen des Herbarium Hooker in Kew [etc.]. Flora 47: 433-441, 465-471, 481-487, 513-520, 529-540. 1864.
- . Systemen der Euphorbiaceen. Bot. Zeit. 22: 324. 1864.
- . Euphorbiaceae [except Euphorbieae]. DC. Prodr. 15(2): 189-1261, 1269-1286. 1866.
- . Nachschrift zu meiner systematischen Arbeit über Euphorbiaceen. Bot. Zeit. 24: 333-345. 1866.
- . Euphorbiaceae. In: C. F. P. MARTIUS, Fl. Brasil. 11(2): 1-292. *pls.* 1-42. 1873; 293-750. *pls.* 43-104. 1874.
- MURLEY, M. Distribution of Euphorbiaceae in Iowa, with seed keys. Iowa State Coll. Jour. Sci. 19: 415-427. 6 maps. 1945.
- NAIR, N. C., & V. ABRAHAM. Floral morphology of a few species of Euphorbiaceae. Proc. Indian Acad. Sci. B. 56: 1-12. 1962. [*Breynia*, *Codiaeum*, *Croton*, *Hevea*, and *Jatropha*.]
- NOZERAN, R. Sur quelques fleurs mâles d'Euphorbiacées. Rec. Trav. Lab. Bot. Univ. Montpellier Bot. 6: 99-114. 1953. [Mostly Hippomaneae and Euphorbieae.]
- O'DONELL, C. A., & A. LOURTEIG. Chrozophoreae Argentinae. Lilloa 8: 37-81. *pls.* 1-7. 1942. Hippomaneae Argentinae (Euphorbiaceae). *Ibid.* 545-592. *pls.* 1-6.
- PAX, F. Die Anatomie der Euphorbiaceen in ihrer Beziehung zum System derselben. Bot. Jahrb. 5: 384-421. *pls.* 6, 7. 1884.
- . Euphorbiaceae. Nat. Pflanzenfam. III. 3(5): 1-119. 2 *pls.* 1890. Nachträge zu Teil III. Abt. 5: 210-213. 1897; *Ibid.* 37, 38. 1900; *Ibid.* (Ergänzungshefte II): 191-195. 1906-1907; *Ibid.* (Ergänzungsheft III): 166-185. 1914.
- . Einige neue Euphorbiaceen aus Amerika. Repert. Sp. Nov. 8: 161, 162. 1910.
- . Die Phylogenie der Euphorbiaceae. Bot. Jahrb. 59: 129-182. 1924.
- . Euphorbiaceae americanae novae II. Repert. Sp. Nov. 41: 224-226. 1937.
- & K. HOFFMANN. Euphorbiaceae. Pflanzenreich IV. 147-[I], II-VII, IX-XVII. 1910-1924. [I.] Jatrophaeae (Heft 42): 1-148. 1910; II. Adrianeae, Additamentum I (Heft 44): 1-111. 1910; III. Cluytieae, Additamentum II (Heft 47): 1-124. 1911; IV. Gelonieae (Heft 52): 1-41. 1912; V. Hippomaneae, Additamentum III (Heft 52): 1-319. 1912; VI. Acalypheae-Chrozophorinae, Additamentum IV (Heft 57): 1-142. 1912; VII. Acalypheae-Mercurialinae, Additamentum V (Heft 63): 1-473. 1914; IX. Acalypheae-Plukenetiinae (Heft 68): 1-108. 1919; X. Acalypheae-Epiprinae (Heft 68): 109-111. 1919; XI. Acalypheae-Ricininae (Heft 68): 112-134. 1919; XII. Dalechampieae (Heft 68): 1-59. 1919; XIII. Pereaee (Heft 68): 1-14. 1919; XIV. Additamentum VI (Heft 68): 1-81. 1919; XV. Phyllantheae (Heft 81): 1-349. 1922; XVI. Acalypheae-Acalyphinae,

- Additamentum VII (Heft 85): 1-231. 1924. [Incomplete; no treatments published of Phyllanthae subtribes Phyllanthinae and Glochidiinae, Crotonaeae, and Euphorbieae. Parts I and II by Pax alone.]
- & ———. Systematische Stellung der Gattung *Aextoxicon*. Jahresber. Schles. Ges. Vaterl. Cult. 1916(Bd.I, Abt.II.b.): 17-21. 1917. [Refers *Aextoxicon* to a separate family.]
- & ———. Euphorbiaceae. In: O. VON KIRCHNER, E. LOEW, & C. SCHRÖTER, Lebensgeschichte der Blütenpflanzen Mitteleuropas 3(3): 241-308. 1930.
- & ———. Euphorbiaceae. Nat. Pflanzenfam. ed. 2, 19c: 11-233. 1931.
- PERRY, B. A. Cytological relationships in the Euphorbiaceae. Virginia Jour. Sci. 3: 140-144. 1943 ("1942").
- . Chromosome number and phylogenetic relationships in the Euphorbiaceae. Am. Jour. Bot. 30: 527-543. 1943.
- POLHAMUS, L. G. Rubber. Botany, production, and utilization. xvii + 448 pp. pls. 1-64. London. 1962. [Includes discussions of *Hevea*, *Manihot*, and other laticiferous Euphorbiaceae.]
- POTBURY, S. S. The La Porte flora of Plumas County, California. Carnegie Inst. Publ. 465: 29-81. pls. 1-18. [Four dubious taxa of Euphorbiaceae, 74-76.]
- PUNT, W. Pollen morphology of the Euphorbiaceae with special reference to taxonomy. Wentia 7: 1-116. 1962.
- RAJU, M. V. S., & A. N. RAO. The development of the male and female gametophytes in *Mallotus albus* Mull. Half-yearly Jour. Mysore Univ. II. B. 13: 5-8. 1952. [Reports *Drusa*-type embryo sac as found by Ventura in *M. japonicus*.]
- RAMANUJAM, C. G. K. Fossil woods of Euphorbiaceae from the Tertiary rocks of South Arcot District, Madras. Jour. Indian Bot. Soc. 35: 284-307. 1956. [Describes 3 new genera: *Bridelioxylon*, *Glochidioxylon*, and *Putranjivoxyton*.]
- RECORD, S. J. The American woods of the family Euphorbiaceae. Trop. Woods 54: 7-40. 1938.
- RITTERSHAUSEN, P. Anatomisch-systematische Untersuchung von Blatt und Axe der Acalypheen. Inaug.-diss. 123 pp. 1 pl. Munich. 1892.
- ROTHDAUSCHER, H. Ueber die anatomischen Verhältnisse von Blatt und Axe der Phyllantheen (mit Ausschluss der Euphyllantheen). Bot. Centralbl. 68: 65-79, 97-108, 129-136, 161-169, 193-203, 248-253, 280-285, 305-315, 338-346, 385-393. 1896. [Also published as repaged diss., 89 pp. Cassel. 1896.]
- SANTOS, J. K. The laticiferous vessels and other anatomical structures of *Excoecaria Agallocha*. Philip. Jour. Sci. 47: 295-304. pls. 1-3. 1932.
- SCHULTES, R. E. Studies in the genus *Hevea*. I. Bot. Mus. Leaflet. Harvard Univ. 13: 1-11. 1947; II. *Ibid.* 97-132. pls. 8, 9. 1948; III. *Ibid.* 14: 79-86. pls. 18, 19. 1950; V. *Ibid.* 15: 247-254. 1952; VI. *Ibid.* 255-272. pls. 77-79.
- . Studies in the genus *Micrandra* I. The relationship of the genus *Cunuria* to *Micrandra*. *Ibid.* 201-221. pls. 65-74. [Reduces *Cunuria* to *Micrandra*.]
- . A note on the genus *Joannesia*. *Ibid.* 17: 25, 26. 1955. [*J. insolita* Pitt. reduced to a synonym of *J. princeps*.]
- . A new generic concept in the Euphorbiaceae. *Ibid.* 27-36. pls. 12-14. [*Vaupesia cataractarum* Schult.; related to *Joannesia*.]

- SCHWEIGER, J. Beiträge zur Kenntnis der Samenentwicklung der Euphorbiaceen. *Flora* 94: 339-379. 1905.
- SCOTT, D. H. On the occurrence of articulated laticiferous vessels in *Hevea*. *Jour. Linn. Soc. Bot.* 21: 566-573. 1885. [Points out differences between laticiferous organs of *Hevea* and *Manihot* vs. those of *Jatropha*.]
- SHERFF, E. E. Additional studies of the Hawaiian Euphorbiaceae. *Publ. Field Mus. Bot.* 17: 547-576. 1939. [Includes a revision of Hawaiian *Claoxylon*, reduction of *Neowawrea* to *Drypetes*.]
- SINGH, R. P. Forms of ovules in Euphorbiaceae. Pp. 124-128 in *Plant Embryology, a symposium*. vi + 273 pp. New Delhi. 1962.
- . Structure and development of seeds in *Codiaeum variegatum* Blume. *Jour. Indian Bot. Soc.* 44: 205-210. 1965.
- SMITH, J. J. Euphorbiaceae. In: KOORDERS & VALETON, *Addim. Cogn. Fl. Arb. Java*. 12: 9-637. 1910. [A critical regional monograph; in Dutch and Latin.]
- SOLEREDER, H. Systematic anatomy of the dicotyledons. Vol. II. Monochlamydeae. (Transl. L. A. BOODLE & F. E. FRITSCH.) vi + pp. 645-1182. Oxford. 1908. [Euphorbiaceae, 739-763, 1047-1055.]
- THATACHAR, T. Morphological studies in the Euphorbiaceae. *Half-yearly Jour. Mysore Univ. II. B.* 13: 43-68. 1953. [Mainly embryological studies of spp. of *Breynia*, *Croton*, *Euphorbia*, *Putranjiva*, and *Sebastiania*.]
- THORNE, R. F. Vascular plants previously unreported from Georgia. *Castanea* 16: 29-48. 1951. [Includes *Aleurites*, *Manihot*.]
- UPHOF, J. C. T. Certain minor rubber producing plants in the Western Hemisphere during times of emergency. Pp. 201, 202 in F. VERDOORN, ed., *Plants and plant science in Latin America*. Waltham, Mass. 1945. [Discusses spp. of *Sapium*, *Cnidoscolus*, and *Euphorbia*.]
- VENTURA, M. Sulla poliembrionia di *Mallotus japonicus* Muell. *Arg. Ann. Bot. Roma* 20: 568-578. pls. 15, 16. 1934. [Embryo sac 16-nucleate *Drusa* type.]
- . Nuovo contributo alla embriologia delle Euforbiacee. *Ibid.* 22: 42-52. pls. 5-7. 1940. [Studies of *Euphorbia*, *Sapium*, and *Manihot*.]
- VINDT, J. Monographie des Euphorbiacées du Maroc. Première Partie. Revision et systématique. *Trav. Inst. Sci. Chérifien* 6: i-xx, 1-217. pls. 1-3. fold. map. 1953. Deuxième Partie. Anatomie. *Ibid.* 19: i-xxix, 219-533. 1960.
- WARMKE, H. E. Studies on pollination of *Hevea brasiliensis* in Puerto Rico. *Science* 113: 646-648. 1951.
- . Studies on natural pollination of *Hevea brasiliensis* in Brazil. *Ibid.* 116: 474, 475. 1952. [Reports that major pollinating agents are Heleid midges.]
- WEBSTER, G. L. The status of *Agyneia* and *Glochidion*. *Taxon* 9: 25, 26. 1960. [*Glochidion* proposed for conservation.]
- . A revision of the genus *Meineckia*. *Acta Bot. Neerl.* 14: 323-365. 1965. [Includes discussion of generic relationships in part of Phyllanthaceae.]
- & J. R. ELLIS. Cytotaxonomic studies in the Euphorbiaceae, subtribe Phyllanthinae. *Am. Jour. Bot.* 49: 14-18. 1962.
- & K. I. MILLER. The genus *Reverchonia* (Euphorbiaceae). *Rhodora* 65: 193-207. 1963. [Discusses systematic importance of ovular morphology in subfam. Phyllanthoideae.]
- WHEELER, L. C. A miscellany of New World Euphorbiaceae. [I.] *Contr. Gray Herb.* 124: 35-42; II. *Ibid.* 127: 48-77. pls. 3, 4. 1939.

- . Dichapetalaceae et Euphorbiaceae novae. Proc. Biol. Soc. Wash. 53: 7-11. 1940.
- WILLIAMS, L. Woods of northeastern Peru. Publ. Field Mus. Bot. 15: 1-587. 1936. [Euphorbiaceae, 264-283.]
- ZIMMERMANN, W. G., G. HEGI, & H. BEGER. Euphorbiaceae. In: HEGI, Illus. Fl. Mittel-Europa 5(1): 113-193. pls. 177, 178. 1923. [*Mercurialis*, *Euphorbia*; includes original morphological observations by Zimmermann.]

## KEY TO THE GENERA OF EUPHORBIACEAE

- A. Ovules paired in each locule of the ovary; sap never milky; leaves not glandular; flowers axillary, solitary or in glomerules, not in spikes; pollen (in local taxa) mostly tricolporate (Subfam. Phyllanthoideae).
- B. Disc in male flower extrastaminal; flowers with or without petals; fruit dehiscent, or at least with more than 1 seed.
- C. Plants dioecious; petals present; rudimentary gynoecium evident in male flower.
- D. Male flowers sessile; pollen with short colpi; trees or arborescent shrubs with leathery leaves. . . . . 1. *Savia*.
- D. Male flowers pedicellate; pollen with elongated colpi; subshrubs or herbs, leaves with thinner texture. . . . . 2. *Andrachne*.
- C. Plants monoecious (in most species); petals absent; male flower without a rudimentary gynoecium.
- E. Disc usually present in both sexes; male calyx open at anthesis, lobes not inflexed; seeds with dry coat, lacking a ventral invagination. . . . . 3. *Phyllanthus*.
- E. Disc absent; male calyx turbinate, lobes connivent-inflexed; seeds with somewhat fleshy coat, ventrally invaginated. . . . . [*Breynia*.]
- B. Disc in male flower intrastaminal, at least in part; flowers apetalous; fruit indehiscent, seeds one per locule; dioecious trees or shrubs with coriaceous leaves. . . . . 4. *Drypetes*.
- A. Ovules solitary in each locule of the ovary; sap often milky or colored; leaves sometimes with petiolar or laminar glands; pollen tricolporate or inaperturate (Subfam. Crotonoideae).
- F. Flowers solitary, spicate, or in cymes, not in bisexual pseudanthia.
- G. Inflorescence dichasial or else stamens inflexed in the bud; petals present or else calyx petaloid; pollen spheroidal, verrucose, porate or inaperturate [tricolporate in *Hevea*].
- H. Stamens scarcely or not at all inflexed in the bud; trichomes simple and uniseriate, rarely stellate or lepidote; inflorescence dichasial.
- I. Perianth biseriate; pollen inaperturate; stem exudate colored, not a milky latex.
- J. Calyx lobes free, imbricate; fruit capsular; seeds carunculate; stipules more or less persistent. . . . . 5. *Jatropha*.
- J. Calyx lobes valvate, fused into a spathe; fruit indehiscent, seeds ecarunculate; stipules caducous. . . . . 6. *Aleurites*.
- I. Perianth uniseriate; pollen aperturate; stems exuding milky latex when cut.
- K. Pollen tricolporate; seeds ecarunculate; leaves compound. . . . . [*Hevea*.]

- K. Pollen porate; seeds carunculate; leaves often deeply lobed but usually not compound.
- L. Male disc intrastaminal; stamens free; male perianth usually yellowish, greenish, or purplish; stinging hairs absent. . . . . 7. *Manihot*.
- L. Male disc extrastaminal; stamens connate; male perianth white; stinging hairs present . . . . . 8. *Cnidoscolus*.
- H. Stamens more or less inflexed in the bud; trichomes often stellate or lepidote; inflorescence racemiform or spiciform; pollen inaperturate.
- M. Fruit a dehiscent, 3-locular schizocarp; seeds carunculate. . . . . 9. *Croton*.
- M. Fruit indehiscent, unilocular; seeds ecarunculate. . . . . 10. *Crotonopsis*.
- G. Inflorescence not clearly dichasial (mostly racemiform or spiciform); petals absent or, if present, then male calyx valvate; pollen various, mostly tricolporate, never verrucose.
- N. Petals present, at least in male flower; seeds ecarunculate; calyx lobes valvate.
- O. Rudimentary gynoecium present in male flower; trichomes simple or glandular (not malpighiaceus); leaves finely serrate, lateral veins distinctly parallel. . . . . 11. *Caperonia*.
- O. Rudimentary gynoecium absent; trichomes malpighiaceus (at least in part); leaves entire or coarsely serrate, veins not distinctly parallel. . . . . 12. *Argythamnia*.
- N. Petals absent in the male flower.
- P. Male calyx valvate; sap watery; styles conspicuously papillate to lacinate (or, if not, then plants with stinging hairs).
- Q. Stamens free or connate, not branched or fasciculate; anthers mostly less than 10 per flower; leaves pinnately veined, at most slightly lobed; stipules discrete, not united; inflorescence spiciform, racemiform, or capitulate; female flowers proximal to the male.
- R. Styles lacinate or pinnatifid; herbs or shrubs, never twining; stinging hairs absent; seeds usually carunculate.
- S. Leaves opposite; plants usually dioecious; bracts small; anthers not much elongated; female flower with 2 elongated staminodia; carpels usually 2. . . . . 13. *Mercurialis*.
- S. Leaves alternate; plants monoecious (in local taxa); female bracts enlarged; anthers elongated, vermiform; female flower lacking staminodia; carpels usually 3. . . . . 14. *Acalypha*.
- R. Styles unlobed, at most papillate; herbs, often twining, armed with stinging hairs; seeds not carunculate. . . . . 15. *Tragia*.
- Q. Stamens branched and fasciculate, anthers many (up to 1000) per flower; leaves palmately lobed; stipules fused into a circular sheath; inflorescence paniculate, normally with female flowers distal to the male; seeds carunculate. . . . . 16. *Ricinus*.

- P. Male calyx imbricate or reduced; styles undivided, not lacinate or pinnatifid; female bracts not accrescent; sap often milky; inflorescences spiciform or racemiform.
- T. Styles not connate into a distally enlarged column; male inflorescence not fleshy and conelike; carpels 2 or 3 (except in *Hippomane*).
- U. Seeds carunculate, dry; fruit capsular.
- V. Floral bracts conspicuously biglandular at base, not displaced from rachis of inflorescence; ovary not conspicuously stipitate.
- W. Columella not 3-horned at base; male calyx lobes and stamens 3; female flowers distinctly pedicellate. . . . . 17. *Sebastiania*.
- W. Columella with a 3-horned gynobase persistent after dehiscence of fruit; male calyx lobes and stamens usually 2; female flower sessile or nearly so. . . . . 19. *Stillingia*.
- V. Floral bracts not glandular at base, adnate to lateral axes of inflorescence (and thus displaced from rachis); ovary conspicuously stipitate. . . . . 18. *Gymnanthes*.
- U. Seeds ecarunculate, either seed coat or carpel wall fleshy.
- X. Fruit thin walled, capsular; seed coat fleshy ('arillate'); ovary 3-locular; styles connate to about the middle. . . . . 20. *Sapium*.
- X. Fruit drupaceous; seed coat dry; ovary 6-10-locular; styles connate only near the base. . . . . 21. *Hippomane*.
- T. Female flower with umbraculiform stigmatic disc terminating a long stylar column; male flowers aggregated into a fleshy pedunculate conelike structure; carpels more than 5. . . . . [*Hura*.]
- F. Flowers aggregated into a usually bisexual cyathium (pseudanthium), usually with one central female flower surrounded by 4 or 5 male monochasia; glands (nectaries) of cyathium usually conspicuous, often with petaloid appendages.
- Y. Cyathia more or less actinomorphic, at least not conspicuously spurred; styles mostly united only below the middle and stems not markedly succulent (in native taxa).
- Z. Leaves alternate or opposite, if opposite, then not inequilateral at base and with chlorenchyma-sheathed veins; main axis not aborting, branching monopodial at least below; stipules often reduced or absent. . . . . 22. *Euphorbia*.
- Z. Leaves entirely opposite, usually distinctly inequilateral at base, stipulate, with chlorenchyma-sheathed veins; main axis aborting just above the cotyledons, branching sympodial throughout. . . . . 23. *Chamaesyce*.
- Y. Cyathia zygomorphic, the glands hidden within a conspicuous spur; styles united most of their length; stems succulent. . . . . 24. *Pedilanthus*.

## Subfam. PHYLLANTHOIDEAE Pax

## Tribe PHYLLANTHEAE [Dumort.]

Subtribe *Andrachninae* Muell. Arg., "Andrachneae"1. *Savia* Willdenow, Linn. Sp. Pl. 4(2): 771. 1806.

Dioecious shrubs or small trees. Leaves alternate, entire, chartaceous to coriaceous, short-petiolate, stipulate. Flowers axillary, the male in dense glomerules, the female few or solitary. Calyx ordinarily 5-parted, lobes imbricate; petals 5, much smaller than sepals [large and conspicuous in some Malagasian taxa]. Male flower: stamens 5, free; anthers introrse, opening longitudinally; pollen subglobose, reticulate, colpi short, endocolpus with diffuse or rounded ends; rudimentary gynoecium 3-lobed. Female flower: disc annular; carpels 3; styles more or less free, bifid, branches slender; ovary glabrous or pubescent; ovules 2 in each locule, anatropous. Fruit capsular; columella persistent; seeds 1 (2) per locule, smooth, chalaza ventral; endosperm copious; embryo straight; cotyledons broad, plane, much longer than the radicle. TYPE SPECIES: *S. sessiliflora* (Sw.) Willd. (Named in honor of Gaetano Savi, 1769–1844, professor at Pisa.)

A genus of 20 to 25 species with a remarkable tricentric distribution: West Indies, southern Brazil, and Madagascar. The circumscription adopted here is approximately that of Bentham and is also near that of Pax and Hoffmann, except that their *Savia phyllanthoides* is returned to *Andrachne*.

Our single representative, *Savia bahamensis* Britton, is a common shrub of coastal and lowland thickets from the Florida Keys south and east to the Bahamas, Caicos Islands, Cuba, Cayman Islands, and Jamaica. It is very similar in appearance to the common Cuban species *S. erythroxyloides* Griseb., from which it differs in its glabrous (rather than sericeous) ovary and its more strongly reticulate leaves (the tertiary veinlets prominent beneath, whereas they are obscure in *S. erythroxyloides*). In these characters it agrees more closely with the Cuban *S. clusiiifolia* Griseb., but that species differs in its more cuneate-truncate leaves and larger seeds.

In the Keys, *Savia bahamensis* has been little collected except on Big Pine Key, although records are available from Little Torch Key, No Name Key, and Key Largo. Possibly the species is often overlooked, as the flowers (which seem to appear mainly in April and May) are relatively inconspicuous. Chromosome counts of the plant would be most desirable since not a single species of *Savia* has ever been reported on cytologically.

According to the classification proposed by Urban, *Savia bahamensis* would fit into sect. HETEROSAVIA Urb., characterized by fruits with 2-seeded locules and an embryo with the radicle about half as long as the cotyledons. In this circumscription, sect. SAVIA is monotypic, containing only *S. sessiliflora*, which has capsules with 1-seeded locules (the second ovule abortive in development). This difference is not absolute, however, since the

seeds in various species of sect. HETEROSAVIA are often of different sizes and in some instances are probably not viable. However, other characters (e.g., leaf texture, petal size) are correlated with this difference, and Urban's proposed distinction may well be valid.

The biseriate perianth, unspecialized pollen, and generalized vegetative characteristics of *Savia* mark it as one of the more primitive taxa of Euphorbiaceae. Although Rothdauscher reported vessels with simple perforations in *S. sessiliflora*, Solereder found scalariform perforations in other species. Our own species, *S. bahamensis*, appears to be rather highly specialized, since it has simple vessel perforations and mostly uniseriate rays. Comparisons with the Madagascar species are much needed. Köhler has noted that *Savia* is palynologically heterogeneous even after some extraneous taxa brought in by Pax are excluded. Most of the primitive taxa in subtribe Andrachninae have oblate spheroidal grains, as found in the West Indian *S. sessiliflora* and *S. andringitrana* Leandri from Madagascar. However, in *S. Danguyana* Leandri of sect. PETALODISCUS and in species of the West Indian HETEROSAVIA (e.g., *S. erythroxyloides*), the grains are prolate and have a much finer ornamentation.

*Savia* cannot be delimited satisfactorily until the Madagascar species are carefully studied. It is notable that these plants differ from the West Indian ones in being monoecious and having a more conspicuous disc; further study may show that they should be segregated into a separate genus, *Petalodiscus*, as was done by Pax in 1890. This would make *Savia* an entirely American group but would not affect the obvious affinity between the West Indian and Malagasian taxa. The evidence from pollen characters, in fact, seems contradictory, since it suggests two groups of affinity, each represented in both the West Indies and in Madagascar. Examination of seeds in the Madagascar taxa might possibly help to resolve the impasse. Leandri has reported exalbuminous seeds in the Madagascar species *S. Bojeriana* Baill., whereas in all West Indian plants examined copious endosperm is present. If a correlation between seed and pollen classes can be established, the circumscription of the subgeneric taxa in *Savia* can at last be fixed.

Whatever the circumscription of *Savia* may prove to be, the genus certainly belongs in the taxonomic group which includes woody Old World genera such as *Blotia* and *Wielandia*. Its only near relative in the New World (and a rather distant one at that) would appear to be *Astrocasia*, which differs strikingly in appearance due to its long-petiolate leaves and more conspicuously petaliferous flowers; the extrorsely dehiscent stamens adnate to the vestigial gynoeceum in *Astrocasia* furnish an additional technical distinction. The genus *Andrachne* is difficult to distinguish from *Savia* on a world-wide basis because of the variability of both taxa, although Köhler has shown that the pollen is quite different, and at least the typical species of *Andrachne* have hemitropous ovules. The local representatives of the two genera may be easily distinguished by the larger and thicker leaves, sessile male flowers, and solitary seeds of *Savia*.



## REFERENCES:

Under family references see BAILLON (1858), GAUCHER, KÖHLER, LEANDRI, PUNT, RECORD, ROTHDAUSCHER, and SOLEREDER.

PAX, F., & K. HOFFMANN. Euphorbiaceae-Phyllanthoideae-Phyllanthaceae-Wielandiiinae. Pflanzenreich IV. 147-IX (Heft 81): 180-189. 1922.

URBAN, I. Nova genera et species II. Symb. Antill. 3: 280-420. 1920. [Description of sect. *Heterosavia*, 284.]

———. Sertum antillarum XXX. Repert. Sp. Nov. 28: 209-236. 1930. [Describes several spp. of *Savia* and discusses relationships of *S. bahamensis*, 209-212.]

2. **Andrachne** Linnaeus, Sp. Pl. 2: 1014. 1753; Gen. Pl. ed. 5. 444. 1754.

Herbs or subshrubs. Leaves alternate, stipulate, petioles abbreviated to as long as the blade; blades thin, entire, often small. Plants dioecious [in our representative, most other species monoecious]; flowers in axillary clusters, the female often solitary. Flowers petaliferous, but petals often reduced or (in the female flower) rudimentary; disc usually segmented (except in our representative). Male flower: stamens 5, opposite the calyx lobes; filaments free [sometimes united]; anthers introrse or laterally dehiscent; pollen more or less prolate, 3-colporate, colpi elongate, endocolpus pointed at ends; vestigial gynoecium usually lobed or divided. Female flower: carpels 3; stigmas capitate; styles more or less free, spreading, bifid; ovary glabrous or pubescent; ovules 2 in each locule, anatropous [or transitional to hemitropous]. Fruit capsular; columella persistent. Seeds usually 2 in each mericarp, smooth or roughened; endosperm copious; embryo straight, cotyledons not folded, broader than the radicle.  $2n = 24, 26$ . (Including *Lepidanthus* Nutt.) LECTOTYPE SPECIES: *A. Telephioides* L.; see Small in Britton & Brown, Illus. Fl. No. U. S. ed. 2. 2: 453. 1913. (Name from Greek, *andrachne*, supposedly applied to *Portulaca oleracea* L. by ancient authors.)

As here delimited in the sense of Mueller, *Andrachne* is a small but distinctly heterogeneous genus of approximately 15 species widely scattered in both temperate and tropical regions of the Old World and New World. Only four species are known in North America; a single one, *A. phyllanthoides* (Nutt.) Coulter,  $2n = 26$ , enters our area.

Until recently, this species was unknown east of the Mississippi, the outlying localities being in southern Missouri (Texas and Shannon counties) and central Arkansas (Garland, Saline, and Hot Springs counties). In 1963, Mrs. Blanche Dean discovered a colony along the banks of Scarum Creek in Blount County, Alabama; according to Mrs. Dean the plant here grows in deep sand among boulders in association with *Rhus radicans*, *Salix nigra*, and *Amorpha fruticosa*. In the western parts of its range (Texas and Oklahoma), *A. phyllanthoides* appears to be an obligate calciphile, usually growing in cracks in limestone; at the same time, however, it does seem to prefer creekbed localities which are periodically flooded. In central Arkansas, on the other hand, Demaree (on labels) reports finding it on steep shale or novaculite slopes.

The discovery of the Blount County station, over 300 miles east of the nearest population, adds another interesting relict to the ones already known from central and northern Alabama and recalls the extreme restriction of *Croton alabamensis* in the Warrior and Cahaba River basins. The Alabama plants seem taxonomically indistinguishable from those farther west, although they may prove to have certain minor differences (viz., possibly smaller petals) when the population is better sampled. No other species of this family in the Southeast shows such an outstanding disjunction, although the bicentric population (Texas-Florida) of *Phyllanthus abnormis* and the vicariant pair *P. polygonoides-platylepis* (Texas-Louisiana and northwestern Florida) offer somewhat analogous distribution patterns. The relatively slight morphological differentiation which has occurred in all three instances suggests that the disjunctions may date only to the Pleistocene.

Within the genus *Andrachne*, *A. phyllanthoides* appears to be quite isolated, except for its western vicariant *A. arida* (Warnock & Johnston) Webster.<sup>5</sup> This latter plant, which is known only from a few desert localities in trans-Pecos Texas and Coahuila, obviously resembles *A. phyllanthoides* but differs in its shrubbier habit, smaller more rigid leaves, and shorter pedicels. As Warnock and Johnston suggest, the two species appear to represent the vicarious offspring of an originally widespread and continuous population the range of which has been dissected by climatic change.

This species-pair (*A. phyllanthoides-arida*) occupies a taxonomically isolated position within *Andrachne*. The smooth, anatropous seeds and dioecious inflorescences suggest *Savia*, where, in fact, both species have been placed by most recent workers. However, Punt and Köhler have shown that the pollen grains of *A. phyllanthoides*, with elongate colpi and large, sharply defined ora, resemble those of typical species of *Andrachne* much more than they do any species of *Savia*. Furthermore, in habit and in gross flower structure both species show a much greater resemblance to the Asiatic species of *Andrachne* sect. ARACHNE Endl. than to any species of *Savia*.

Some contemporary workers (e.g., Hurusawa, Pojarkova) accept *Arachne* as a distinct genus from *Andrachne* (sensu stricto) and would presumably place *A. phyllanthoides* in *Arachne*. However, in most characteristics the latter taxon is so close to typical representatives of *Andrachne* that it would be difficult and inconvenient to recognize two genera. In tackling this problem in the future, notice should be taken of the relatively neglected feature of ovule configuration: at least some taxa of sect. ARACHNE have anatropous ovules, whereas in *A. Telephioides* (§ AN-

<sup>5</sup> *Andrachne arida* (Warnock & Johnston) Webster, comb. nov. *Savia arida* Warnock & Johnston, Southw. Nat. 5: 3. 1960. This new combination is rather embarrassing to the author, since it was at least partly on his advice that Warnock and Johnston described their plant as a *Savia* rather than as an *Andrachne*. Since then, however, accumulating evidence shows that their plant must be excluded from *Savia*, and the most conservative course is to place it in *Andrachne*, rather than in some segregate genus.

DRACHNE) they are hemitropous. However, it is not yet certain whether this difference will hold for other species assigned to *Andrachne*. For the time being, therefore, it appears that the best disposition of the two species of the United States is still that of Mueller, who placed *A. phyllanthoides* in *Andrachne* as the only representative of section PHYLLANTHOPSIS (Scheele) Muell. Arg., characterized by the undissected male disc, somewhat woody habit, and deeply divided vestigial gynoeceum.

According to both Köhler and Punt, *Andrachne* is palynologically similar to the Old World genus *Actephila*; an affinity between these two genera was pointed out long ago by Baillon. However, *Actephila* differs markedly from all species of *Andrachne* in its seeds, which are solitary (by abortion) in each locule and nearly or quite without endosperm, the cotyledons more or less folded. Through sects. ARACHNE and PHYLLANTHOPSIS, *Andrachne* seems more closely related to *Savia*, of which it may be regarded as the herbaceous derivative (cf. *Savia* for generic distinctions). In another direction, *Andrachne* stands in approximately an ancestral position to various apetalous genera of subtribe Phyllanthinae. For example, *A. ovalis* of South Africa has many of the attributes of the hypothetical ancestor of both *Meineckia* and *Chascotheca*, while *A. Telephioides* and its relatives show a possible significant resemblance to some nearctic herbaceous species of *Phyllanthus* subg. ISOCLADUS. From all of these genera *Andrachne* may be distinguished by its diminutive habit, delicate petaliferous flowers, characteristic pollen grains, and paired seeds with copious endosperm.

#### REFERENCES:

- Under family references see ASSAILLY, CROIZAT (1943), GAUCHER, HURUSAWA, KÖHLER, MICHAELIS, PUNT, ROTHDAUSCHER, and VINDT.
- CLARK, R. C. *Andrachne phyllanthoides* (Nuttall) Muell. on the Cumberland Plateau of Alabama. *Castanea* 32: 73, 74. April 1967. [Reports a visit in Aug. 1966 to the Blount County station.]
- JOHNSTON, M. C. *Savia arida* in Coahuila, Mexico. *Southwest. Nat.* 7: 80. 1962.
- PAX, F., & K. HOFFMANN. Euphorbiaceae-Phyllanthoideae-Phyllanthaceae-Andrachninae. *Pflanzenr.* IV. 147-XV (Heft 81): 169-179. 1922.
- POJARKOVA, A. I. Contribution à la systématique des représentants du genre *Andrachne* s. l. habitant le Caucase et la partie de la région méditerranéenne. (In Russian.) *Bot. Zhur.* 25: 341-348. 1940.
- REESE, G. Über die Polyploidiespecktren in der nordsaharischen Wüstenflora. *Flora* 144: 598-634. 1957. [Reports chromosome number of *A. Telephioides*.]
- WARNOCK, B. H., & M. C. JOHNSTON. The genus *Savia* (Euphorbiaceae) in extreme western Texas. *Southwest. Nat.* 5: 1-6. 1960.

#### Subtribe Drypetinae Griseb., "Drypeteae"

### 3. *Drypetes* Vahl, *Eclog. Am.* 3: 49. 1810.

Dioecious trees or shrubs, usually with dense wood. Leaves alternate, short-petiolate, stipulate, blades often leathery, entire or sharply toothed,

Flowers in dense axillary clusters, sometimes almost sessile. Flowers apetalous; calyx in both sexes of 4 or 5 (rarely 6 or 7) more or less deciduous imbricate sepals. Male flower: disc intrastaminal, marginal lobes sometimes projecting between stamens; stamens 3–12 (rarely up to 50), filaments free, anthers basifixed and extrorse to introrse; pollen prolate, tricolporate, tectate, with large endocolpus; rudimentary gynoecium present or absent. Female flower: disc cupuliform; ovary of 1 or 2 [very rarely 3 or 4] carpels; styles nearly obsolete, the more or less dilated stigmas nearly sessile atop the ovary; ovules 2 in each locule, anatropous. Fruit indehiscent, becoming more or less drupaceous, exocarp fleshy or leathery, endocarp crustaceous or bony; seeds usually solitary in each locule, ecarunculate, testa smooth; endosperm copious; embryo straight, cotyledons broad. (Including *Cyclostemon* and *Hemicyclia*.) TYPE SPECIES: *D. glauca* Vahl. (Name from Greek, *dryppa*, overripe olive, in allusion to the fruit of the type species.) — GUIANA PLUM, WHITE WOOD.

Perhaps 150 species of circumtropical distribution, the vast majority in the Old World. Originally founded on a West Indian species, *Drypetes* was restricted by Mueller (1866) to American taxa, while related Old World species were assigned to *Cyclostemon* and *Hemicyclia*. However, Pax and Hoffmann (1922) appear to have combined these taxa correctly into a single genus characterized by an indehiscent fruit with reduced seed number, abbreviated styles, and an intrastaminal male disc. Hurusawa (1954) has even combined *Putranjiva* and *Drypetes*, and it must be admitted that the former scarcely differs in any essential character, except its lack of an intrastaminal disc.

Approximately eight or nine species of *Drypetes* are known from the West Indies and Central America. Two, each belonging to a different section, have entered the United States. Representing sect. OLIGANDRAE Pax and Hoffm. is *D. lateriflora* (Sw.) Urb., which normally has only four stamens isomerous with a four-lobed calyx, and a two-locular ovary which develops into a thin-walled, subglobose, scarcely fleshy fruit. It is fairly common in hammocks throughout the Florida Keys and extends northward on the Atlantic coast of Florida as far as Brevard County. Since all the other species<sup>6</sup> of sect. OLIGANDRAE are restricted to the Old World (mainly Africa), the relationships of *D. lateriflora* provide an interesting problem. Further study may show that it should be relegated to a different section.

Section DRYPETES (§ *Hemicyclia* of Pax & Hoffmann), with 30–40 species, includes all the remaining American species of *Drypetes*, among them our other local species, *D. diversifolia* Krug & Urb. (including *D. keyensis* Krug & Urb.). This plant differs greatly from *D. lateriflora* in having a five-lobed calyx, eight to ten stamens, and a one-locular ovary which develops into an oblong drupe with thick exocarp and endocarp.

<sup>6</sup> The only other American species placed in sect. OLIGANDRAE by Pax & Hoffmann is the imperfectly known Cuban *Drypetes triplinervia* Muell. Arg. (DC. Prodr. 15(2): 456. 1866), which must be excluded from *Drypetes* because of its dehiscent fruit. It is properly classified as *Chascotheca triplinervia* (Muell. Arg.) Webster, comb. nov.

The species can ordinarily be easily distinguished in the vegetative state since *D. lateriflora* has thinner leaves which are abruptly pointed at the tip, whereas the leaves of *D. diversifolia* are thicker, more rigid, and mostly rounded to obtuse (or at least not abruptly narrowed) at the tip. Furthermore, *D. diversifolia* shows an interesting leaf polymorphism. Particularly on seedlings and sprout-shoots, the leaves may be conspicuously spinulose-serrate, contrasting greatly with the "normal" entire leaves; some individual branches of a mature tree with entire leaves may show the toothed kind. No such variation occurs in *D. lateriflora*, which always has entire leaves.

Longwood reports that *D. Brownii* Standl., bullhoof, of British Honduras produces strong, hard timber with some of the properties of English oak; it is used for railway ties, rafters, beams, and other heavy construction. No studies of the timber quality of the two Florida species have been reported, but it seems doubtful that they can ever be of any commercial value because of their small size in our area (trunks not over one foot in diameter). The dense wood of *Drypetes*, which makes it potentially valuable for lumber, is correlated with characteristics of considerable systematic interest. The vessels have scalariform perforations, xylem parenchyma is abundant, and fibers are thick-walled. Janssonius grouped *Drypetes* with the Old World genera *Aporosa* and *Baccaurea* on the basis of these characteristics, and Metcalfe and Chalk associated it with the "Aporosa type," from which it is divergent mainly in having rather narrow rays. Anatomically, *Drypetes* appears to be the most primitive of our taxa of Euphorbiaceae, and does not show any close relationship to other local genera of Phyllanthoideae except *Savia*.

Another indication of the taxonomic isolation of *Drypetes* within the Phyllanthoideae is the report by Mangenot & Mangenot of  $2n = 40$  in an African species, *D. mottikoro* Leandri. Chromosome counts are unreported for any American species, but would be of unusual interest, since the one known count suggests a base number ( $x = 10$ ) different from that in most other Phyllanthoideae, which have  $x = 13$ .

Palynologically, *Drypetes* appears to be heterogeneous, for Köhler has recognized two different pollen types within sect. DRYPETES. The closely related genus *Putranjiva*, which Hurusawa has combined with *Drypetes*, has very similar pollen, and *Putranjiva Roxburghii* also has  $2n = 40$  in agreement with the single count in *Drypetes*. Possibly connecting *Drypetes* with taxa in subtribe Andrachninae is *Lingelsheimia*, which Léonard has shown to differ from *Drypetes* by its capsular fruit. Perhaps the most interesting relationship is that of *Drypetes* with the Australian genera *Neoroepera* and *Petalostigma*, which have a similar habit but differ in their monoecious inflorescences, and especially in their pollen grains; because these are porate and echinulate, Köhler refers *Neoroepera* and *Petalostigma* to the subfamily Oldfieldioideae. Although Köhler regards their pollen as derived within the subfamily, the suggestive resemblance to *Drypetes* warrants further analysis, and it seems possible that *Drypetes*

may be the closest surviving taxon to the ancestral stem of the Oldfieldioideae.

#### REFERENCES:

- Under family references see DEHAY, GAUCHER, HURUSAWA, KÖHLER, LEANDRI, LONGWOOD, MICHAELIS, PUNT, RECORD, ROTHDAUSCHER, and SMITH.
- KENG, H. New or critical Euphorbiaceae from eastern Asia. Jour. Wash. Acad. Sci. 41: 200–205. 1951. [Describes *Liodendron*, related to *Drypetes* and *Putranjiva*.]
- LÉONARD, J. Notulae systematicae XXXIII. Sur les limites entre les genres *Drypetes* Vahl et *Lingelsheimia* Pax (Euphorbiacées.) Bull. Jard. Bot. Bruxelles 32: 513–516. 1962.
- PAX, F., & K. HOFFMANN. Euphorbiaceae–Phyllanthoideae–Phyllantheae–Drypetinae. Pflanzenreich IV. 147–XV (Heft 81): 227–280. 1922.
- SARGENT, C. S. *Drypetes*. Silva N. Am. 7: 23–28. pls. 307, 308. 1895.
- URBAN, I. Additamenta ad cognitionem florum Indiae occidentalis. Bot. Jahrb. 15: 286–361. 1892. [Revision of West Indian spp. of *Drypetes*, 351–357.]

#### Subtribe Phyllanthinae [Muell. Arg., "Phyllantheae"]

4. **Phyllanthus** Linnaeus, Sp. Pl. 2: 981. 1753; Gen. Pl. ed. 5. 422. 1754.

Trees, shrubs, or herbs; stems not succulent, often entirely glabrous; lateral axes in some taxa deciduous, subtended by scale-like leaves. Leaves alternate (spiral or distichous), stipulate, pinnately veined, entire and unlobed; petiole short. Plants monoecious or, less commonly, dioecious; inflorescences axillary, cymose, the cymes usually highly condensed and sometimes reduced to solitary flowers. Flowers apetalous; calyx synsepalous, of 4–6 imbricate or decussate lobes; disc usually evident, segmented or cupular. Male flower: disc extrastaminal, usually segmented; stamens (2)3–5 [–15], filaments free or connate; anthers extrorse, dehiscent longitudinally or horizontally; pollen prolate to globose, 3- or 4-colporate [pancolporate or porate in some exotic taxa]; vestigial gynoeceum absent [very rarely present]. Female flower: disc segmented or more often patelliform to cupular [rarely absent]; staminodia absent [very rarely present]; carpels usually 3 [rarely 2 or 4–12]; styles free or basally connate, more or less bifid [rarely entire], sometimes multifid; ovules 2 in each locule, hemitropous, nucellus usually exerted from exostome in contact with obturator; embryo sac normal (*Polygonum*) type. Fruit usually capsular, explosively dehiscent [less commonly baccate or drupaceous]; mericarps separating from a more or less persistent columella; seeds usually 2 in each locule [rarely only one maturing]; testa dry and usually thin [rarely thickened and bony], not ventrally invaginated; endosperm copious; embryo straight or slightly curved, cotyledons broader than and about as long as the radicle. (Including *Cicca* L., *Emblica* Gaertn., *Xylophylla* L.) LECTOTYPE SPECIES: *P. Niruri* L.; see Small in Britton & Brown, Illus. Fl. No. U. S. ed. 2. 2: 453. 1913. (Name from

Greek, *phyllon*, leaf, and *anthos*, flower, in allusion to the production of flowers on specialized leaf-like lateral branches.)

Approximately 750 species may be assigned to this highly diversified genus which is predominantly represented in the Old World tropics. Over 200 species have been reported from America, mostly from Brazil and the West Indies. Less than a dozen attain temperate latitudes, and the genus is unknown in Europe and temperate Pacific America. In the southeastern United States, *Phyllanthus* is represented by eight native and two naturalized species belonging to five sections in three subgenera.

Subgenus ISOCLADUS Webster, which includes about 70 herbaceous species with alternate phyllotaxy and unspecialized ramification patterns, has three Southeastern species. Belonging to section PARAPHYLLANTHUS Muell. Arg. because of their spiral phyllotaxy and dissected floral disc are two closely related species, *Phyllanthus polygonoides* Nutt. ex Spreng.,  $2n = 16$ , and *P. platylepis* Small. A mainly calciphilous plant of limestone regions in Texas and Oklahoma, *P. polygonoides* barely enters our area in prairies of western Louisiana. The very similar *P. platylepis*, which differs mainly in its more or less rhizomatous habit and larger fruits and seeds, is confined to a small region in the hammocks of northwestern Florida (Dixie and Taylor counties). It shows an even more striking resemblance to *P. Liebmannianus* Muell. Arg., of coastal swamps in Veracruz, Mexico. These three species appear to be the vicariant relicts of an ancestral population which probably had a much more nearly continuous distribution along the perimeter of the Gulf of Mexico during the late Tertiary.

The third species of subg. ISOCLADUS, *Phyllanthus caroliniensis* Walt., belongs to sect. LOXOPODIUM Webster by virtue of its distichous phyllotaxy and very short, geniculate fruiting pedicels. This, the most widespread American *Phyllanthus*, is remarkable in being one of the few Euphorbiaceae which is distributed from temperate holarctic regions, south through the tropics into temperate southern latitudes. In the Southeast it is represented by ssp. *caroliniensis*, with smooth stems and an entire or angled female disc, occurring throughout our area except in southern Florida, where it is replaced by ssp. *saxicola* (Small) Webster. The latter taxon, mainly West Indian, has established a beach-head on the mainland only in the Florida Keys and the Dade County pinelands. An extralimital taxon, ssp. *guianensis* (Kl.) Webster, has been shown to have  $2n = 36$ , so that at least two different basic chromosome numbers ( $x = 8, 9$ ) appear to be present in subg. ISOCLADUS.

Subgenus KIRGANELIA (Juss.) Webster, a primarily Old World group, is represented by a single naturalized species, *Phyllanthus tenellus* Roxb.,  $2n = 26$ . This plant native to Africa and the Mascarene Islands belongs to sect. PENTANDRA Webster,<sup>7</sup> which includes about ten herbaceous African

<sup>7</sup> *Phyllanthus* sect. **Pentandra** Webster, sect. nov. Herbae monoicae annuae vel suffruticosae; ramificatione more sectionis *Phyllanthi*; pedicellis capillaribus; flore ♂ calycis lobis 5, disci segmentis distinctis; staminibus 5, liberis; granis pollinis

species with thin-walled capsular fruits, undilated style-branches, and three- or four-colporate pollen grains. The section is significant phylogenetically because most of its taxa have precisely the habit and appearance of species of subg. *PHYLLANTHUS*, from which they scarcely differ in anything more than the five-merous rather than three-merous androecium. Since *P. tenellus* is the only herbaceous diploid species with phyllanthoid branching, it and closely related taxa such as *P. capillaris* Schum. may be regarded as the nearest living equivalents of the taxa ancestral to subg. *PHYLLANTHUS*.

Apparently the earliest collection of *Phyllanthus tenellus* in the United States was made by Hunnewell in Orange County, Florida, in 1924. Since then, however, its spread appears to have been rapid, for it is now known from a considerable number of localities between Sumter County, South Carolina, and Key West. The plant is an aggressive greenhouse weed due to its rapid flowering and effective ballistic seed dispersal; it seems to show a decided preference for sandy soil, and hence is to be found almost ubiquitously in *Citrus* groves in parts of central Florida. Although it has often been confused with native species of subg. *PHYLLANTHUS*, it is easily distinguished by its five free stamens and long capillary fruiting pedicels.

Subgenus *PHYLLANTHUS*, which includes well over 100 species in both hemispheres, comprises herbaceous or suffruticose plants with only two or three stamens and specialized "phyllanthoid" branching; the leaves on the main stem are reduced to scales which subtend deciduous leafy floriferous branchlets. In the Southeast there are five species of this subgenus, two or three of them native. The only representative of sect. *URINARIA* Webster is *Phyllanthus Urinaria* L.,  $2n = 52$ , a weed of Old World origin which has been introduced into a number of localities in the United States during the past 25 years. Although it spreads much less contagiously than *P. tenellus*, it has been found in Texas, Louisiana, and Alabama, and doubtless will be encountered in other Gulf states. While *P. Urinaria* is occasionally confused with taxa of the next section, it differs markedly in its verrucose ovary, sessile female flowers, hispidulous leaf margins, and transversely (rather than longitudinally) ribbed seeds.

Section *PHYLLANTHUS* includes our remaining native species of subg. *PHYLLANTHUS*, characterized by pedicellate flowers, smooth ovaries, and verruculose or longitudinally ribbed or striate seeds. Subsection *NIRURI* Webster, with stamens partially or entirely free, slender scale-leaves, and verruculose seeds, is represented in the United States only by a relict population of *Phyllanthus Niruri* L. in east-central Texas, and does not enter our area. Subsection *SWARTZIANI* Webster, comprising mostly annual plants with connate stamens, broader scale-leaves, and striate or ribbed seeds, includes four local species. *Phyllanthus amarus* Schum.,  $2n = 52$ , the most abundant and widespread weed in the genus, is common in southern Florida (Dade and Monroe counties) and has been collected

---

subglobosis 3- vel 4-colporatis; flore ♀ disco patelliforme, ovario loculis 3, stylis bifidis; fructo capsulare, seminibus asperulis. *TYPUS: Phyllanthus pentandrus* Schum.



as far north as Gadsden County. Because of its nearly ubiquitous distribution, it is impossible to be certain that this species is native to Florida. The closely related *P. abnormis* Baill., which is definitely native, stands extremely close to *P. amarus* morphologically, but can be distinguished by its larger seeds, four-parted male flowers, more deeply dissected female disc, and thicker, more reddish stems. Unlike *P. amarus*, it shows a distinct preference for sandy soils and has a strikingly disjunct range: the western population extends from northeastern Mexico and western Texas to near Houston, while the eastern population is confined to peninsular Florida, from Cedar Key to Dade County. At least one additional species of the subsection, *P. fraternus* Webster, has recently been discovered in Louisiana. It is also very similar in appearance to *P. amarus*, but differs in having the male and female flowers segregated at different axils (in *P. amarus* and *P. abnormis* a male flower is paired with a female at all distal axils on the flowering branchlet).

Subsection PENTAPHYLLI Webster, a West Indian taxon of about 13 or 14 species, characterized by the perennial rootstock and blackened indurate scale-leaves on the main stems, has only a single species in the Southeast: *Phyllanthus pentaphyllus* Wright ex Griseb.,  $2n = 52$ . This is the most widespread species in the subsection, with populations extending from Florida and the Bahamas south to Guadeloupe and Curaçao. The Florida population belongs to ssp. *pentaphyllus* by virtue of its deeply lobed female disc, and it has been distinguished as var. *floridanus* Webster because of its primarily dioecious inflorescences (in contrast to the predominantly monoecious condition in var. *pentaphyllus* of the Bahamas and Cuba). The recent report of *P. pentaphyllus* from South Carolina is erroneous, as it was based on a mislabelled specimen; in the United States the species is confined to limestone areas (mainly pinelands) in Dade and Monroe counties, Florida.

Several other species of *Phyllanthus* have been reported from Florida, but these reports lack confirmation by specimens. Small cited the commonly cultivated *P. acidus* (L.) Skeels, of subg. CICCIA (L.) Webster, from southern Florida, but there is thus far no evidence that it has become naturalized. Small also reported from Key West *P. epiphyllanthus* L., of subg. XYLOPHYLLA (L.) Pers. sect. XYLOPHYLLA, a taxon outstanding because of the branchlets transformed to phylloclades and with concomitant reduction of the leaves to scales. His identification was erroneous, for the specimen from Key West collected long ago by Blodgett, as well as Small's own collection made in 1921, represent *P. angustifolius* (Sw.) Sw., a species otherwise known only from Jamaica and the Cayman Islands. Since the regions closest to Key West (Cuba and the Bahamas) have only *P. epiphyllanthus*, it seems highly unlikely that *P. angustifolius* could have occurred on Key West as a native plant. Recent attempts to locate the species on Key West have been unsuccessful, and it seems most reasonable to conclude that *P. angustifolius*, which was widely planted in Caribbean gardens a century and more ago, became temporarily naturalized and then died out again.

The remarkable amplitude of variation in both vegetative and floral characteristics evident in *Phyllanthus* has led various investigators to propose over 50 segregate genera. However, it has not been demonstrated that the genus is polyphyletic as presently constituted, and there are few large groups of species within it which could be defined by clear-cut diagnostic features. Chromosomal, palynological, and gross morphological characters, although displaying a protean diversity, fail to show the sort of correlation on which segregate genera could easily be justified. For example, the periporate pollen grains of subg. XYLOPHYLLA are correlated with the specialized branching pattern, but in the American species placed in subg. BOTRYANTHUS Webster this type of pollen is associated with definitely nonphyllanthoid branching. Until additional compelling evidence is unearthed, therefore, it seems expedient to maintain the circumscription of *Phyllanthus* as established by Mueller and modified by Hooker (when he recognized *Glochidion* as a separate genus).

The subgeneric classification of *Phyllanthus* is based primarily on characters of branching pattern and pollen, in addition to the usual floral characteristics. In the vast majority of species, an unusual pattern of vegetative development occurs which has been designated as "phyllanthoid branching." In plants of this kind, the main axis produces ordinary leaves only at the first few nodes above the cotyledons; distal nodes have the leaves reduced to scale-like cataphylls subtending deciduous leafy floriferous axes. There is thus a striking division of labor among the portions of the axial system of the plant: permanent axes produce only scale-like leaves and branchlets (never flowers) and are capable of indefinite growth, whereas the lateral axes produce both the leafy and reproductive portions of the plant and are of more or less limited growth (although the terminal bud of the branchlet does not necessarily abort). In a relatively few species, including most of those of temperate regions, such as *P. polygonoides*, there is no such vegetative specialization; flowers and leaves may be produced indiscriminately on both main and lateral axes.

Pollen diversity reaches a development in *Phyllanthus* which among the angiosperms is perhaps rivalled only by that in *Polygonum*. In a rather large number of taxa, the pollen grains are of a relatively unspecialized type similar to those of more primitive genera of Phyllanthaceae such as *Flueggea* and *Securinega*: they are more or less prolate, reticulate, tricolporate, with a well-defined elliptical endocolpus. In a minority of species, mainly in herbaceous taxa of subgenera ISOCLADUS and PHYLLANTHUS, distinctly prolate tectate grains with either three or four colpi have evolved; such microspores somewhat resemble those found in *Antidesma* and related genera. In the woody taxa of subgenera KIRGANELIA and CICCA, on the other hand, occur small more or less globose grains with narrow marginate colpi (often confluent at the poles) and circular endocolpus. It appears that it is from this pollen type that the unusual periporate pollen grains of subg. XYLOPHYLLA have evolved.<sup>8</sup> It is interesting,

<sup>8</sup>These microspores, designated as "synrugoidorate" by Erdtman because the pores are connected by marginate streaks (presumably homologous with the colpi

and probably significant, that the three-colporate syncolpate grains of subg. *KIRGANELIA* and *CICCA* occur in diploid species ( $2n = 26$ ), whereas all known species with periporate grains are at the tetraploid level ( $2n = 52$ ) or higher. Although polyploidy is not necessarily an indication of phylogenetic advancement, the correlation of chromosome number with pollen type and other morphological characters suggests that it does indicate advancement in *Phyllanthus*.

The cytological picture is not a simple and straightforward one, however, since more than one basic number occurs in the genus, and the correlation of karyotypes with morphologically definable taxa is at best imperfect. Until recently, it appeared that the taxa in subg. *ISOCLADUS* were very divergent from other subgenera in having basic numbers of  $x = 8, 9$  instead of  $x = 13$ . Since these plants also had unspecialized branching patterns, in contrast to the phyllanthoid branching found in most of the other subgenera, it might seem that a rather good argument could be presented for the generic segregation of subg. *ISOCLADUS*, including our commonest local species, *P. caroliniensis*. This was not attempted, however, because the flowers in subg. *ISOCLADUS* are so typical for the genus that a segregate genus would be very difficult to characterize morphologically. Furthermore, Miller and Webster (1967) have reported  $x = 9$  in *P. Niruri*, a species with typical phyllanthoid branching (and, in fact, the type species of the taxon including plants with this branching pattern). Although cytological data are still more scanty than one might wish, it now appears that in at least two unrelated lines the basic chromosome numbers of  $x = 8, 9$  have been derived by reduction from the prevailing chromosome complement of  $x = 13$ . This bimodality of chromosome number in *Phyllanthus* appears to be partly explicable on the hypothesis that evolution of the herbaceous habit proceeds in association with a reduction in chromosome number. However, this appears to hold only for species extending into or restricted to temperate regions; tropical herbaceous weeds such as *P. amarus* and *P. Urinaria* show a precisely contrary tendency towards (euploid) polyploidy. Cytological examination of a considerably larger number of herbaceous species will be necessary (and even then possibly not sufficient) to resolve this curious and puzzling picture.

Within the tribe Phyllantheae, *Phyllanthus* is rather well characterized by its apetalous flowers (the male without a rudimentary gynoecium), a distinct floral disc, gynoecia of mostly three carpels with bifid styles, and hemitropous seeds which are not ventrally invaginated. Subgenus *CICCA*, which has been treated as a separate genus by a number of workers, is indeed divergent in the usually indehiscent fruit and often in lacking a floral disc. However, its species have typical phyllanthoid branching and are so similar to certain taxa of subg. *KIRGANELIA* that a generic segrega-

---

in subg. *KIRGANELIA*), possibly evolved as a result of increase in number of colpi in a syncolpate type of pollen grain; mechanical considerations apparently preclude the colpi in syncolpate grains from meeting at the poles if more than three colpi are present.

tion seems neither convenient nor necessary. The closest genus to *Phyllanthus* is the Old World *Glochidion*, which technically differs in its undivided styles and ventrally invaginate seeds. Among the numerous Australian taxa of *Phyllanthus* subg. GOMPHIDIUM<sup>9</sup> are some of uncertain generic status, but it seems probable that additional study will make it possible to define the boundary between the two genera more sharply. It seems fairly clear that *Glochidion* and the smaller Old World genera *Breynia*, *Sauropus*, and *Synostemon* have arisen from *Phyllanthus* subg. KIRGANELIA by loss of floral disc and specialization of seeds, styles, and male perianth. All of these genera together make up the subtribe Phyllanthinae, sensu stricto.

In comparison with many other genera of Euphorbiaceae, *Phyllanthus* includes relatively few species of economic importance; no latex or seed oils, such as are known in the Crotonoideae, occur. *Phyllanthus Emblica* L., a tree with branchlets imitating those of Leguminosae with small leaflets, is an important source of tannin and vitamin C; it is cultivated in the Miami area as an ornamental. Of some potential importance, chemotaxonomically, if not economically, are the alkaloids reported from various species of *Flueggea* and *Margaritaria*, two genera rather closely related to *Phyllanthus*. At least 10 different alkaloids are known at present (Hegnauer), and investigation of the less specialized taxa of *Phyllanthus* may produce data of interest in assessing both intra- and intergeneric relationships. Saponins are known in a number of tropical species of *Phyllanthus*, and may be the active principle in the use of foliage of various species as fish-poisons; South American species of subg. CONAMI appear to be outstanding in this regard. A few species of *Phyllanthus* have some promise as ornamentals in tropical and subtropical gardens. The most popular are probably the xylophyllas, various phylloclade-bearing species of sect. XYLOPHYLLA which have some interest as botanical curiosities. The most common greenhouse xylophylla, *P.* × *elongatus* (Jacq.) Steud., is apparently a hybrid between *P. angustifolius* and *P. epiphyllanthus*. In outdoor gardens in southern Florida, on the other hand, it is the parental species which are commonly grown, and the hybrid appears to be rare.

#### REFERENCES:

- Under family references see ARNOLDI, BAILEY, BAILLON, BANERJI & DUTT, BEILLE in GAGNEPAIN, BENTHAM, DEHAY, ERDTMAN, FROEMBLING, GAUCHER, HUTCHINSON in BROWN, KÖHLER, LEANDRI, LOURTEIG & O'DONELL (1943), McVAUGH, MICHAELIS, MILLER & WEBSTER, MODILEWSKI, PERRY, PUNT, RECORD, SMITH, WEBSTER & ELLIS, WEBSTER & MILLER, WHEELER (1939), and WILLIAMS. AHLs, H. E., C. R. BELL, & A. E. RADFORD. Species new to the flora of North and South Carolina. *Rhodora* 60: 10-32. 1958. [*P. Niruri* and *P. pentaphyllus* erroneously reported from S. Carolina.]  
 ——— & A. E. RADFORD. Species new to the flora of North Carolina. *Jour.*

<sup>9</sup> *Phyllanthus* subg. **Gomphidium** (Baill.) Webster, stat. nov. *Phyllanthus* sect. *Gomphidium* Baill. *Adansonia* 2: 234. 1862. LECTOTYPE SPECIES: *Phyllanthus Chamaecerasus* Baill.

- Elisha Mitchell Sci. Soc. **75**: 140–147. 1959. [Reports *P. Niruri*, erroneously, from New Hanover Co.]
- BAILLON, H. E. Monographie des *Phyllanthus*. Première Partie. Adansonia **1**: 23–43. 1860; **2**: 13–20. 1861. [Never completed; treats only certain American spp.]
- BANCILHON, L. Sur la mise en évidence d'un rôle "organisateur" du méristème apical de l'axe orthotrope de *Phyllanthus*. Compt. Rend. Acad. Sci. Paris **260**: 5327–5329. 1965.
- . Mise en évidence de gradients de différenciation lors du développement végétatif de *Phyllanthus amarus* Schum. et Thonn. *Ibid.* **262**: 1228–1231. 1966.
- , R. NOZERAN, & J. ROUX. Observations sur la morphogénèse de l'appareil végétatif de *Phyllanthus* herbacés. Nat. Monspel. Bot. **15**: 5–12. 1963.
- CROIZAT, L. Three new Amazonian species of *Phyllanthus* L. Trop. Woods **78**: 5–9. 1944. [Includes speculations on inflorescence homologies.]
- DESHPANDE, P. K. Contributions to the embryology of *Kirganelia reticulata* Baill. Jour. Biol. Sci. **2**: 76–83. 1963.
- KAUSSMANN, B. Beiträge zur Morphologie von *Phyllanthus Niruri* L. Planta **38**: 586–590. 1950. [Includes references to earliest reports on phyllanthoid branching.]
- . Histogenetische Untersuchungen zum Flachsprossproblem. Bot. Stud. Jena **3**: 1–136. 1955. [Development of phylloclades in *Phyllanthus*, 97–105.]
- LUDWIG, F. Über das Blühen eines brasilianischen *Phyllanthus* (*Ph. Niruri*?). Kosmos Stuttgart **18**: 35–37. 1886. [Pollination by Diptera.]
- MAHESHWARI, P., & O. R. CHOWDRY. A note on the development of the embryo-sac in *Phyllanthus Niruri* Linn. Curr. Sci. Bangalore **5**: 535, 536. 1937.
- MAJUMDAR, G. P., & M. ARSHAD ALI. Developmental studies of *Phyllanthus Niruri* Linn. and *P. reticulatus* Poir. (Euphorbiaceae) with special reference to the origin and nature of axillary vegetative buds. Proc. Indian Acad. Sci. B. **43**: 149–160. 1956.
- ROBINSON, C. B. Philippine Phyllanthinae. Philip. Jour. Sci. Bot. **4**: 71–105. 1909. [Includes critical review of generic delimitations in the subtribe.]
- SENGUPTA, P., & J. MUKHOPADHYAY. Terpenoids and related compounds — VII. Triterpenoids of *Phyllanthus acidus* Skeels. Phytochemistry **5**: 531–534. 1966. [Reports isolation of phyllanthol, a pentacyclic triterpenoid.]
- SINGH, R. P. Development of endosperm and embryo in *Phyllanthus Niruri* L. Agra Univ. Jour. Res. Sci. **5**: 163–167. 1956. [Sp. probably misdetermined.]
- WEBSTER, G. L. Studies of the Euphorbiaceae, Phyllanthoideae. I. Taxonomic notes on the West Indian species of *Phyllanthus*. Contr. Gray Herb. **176**: 45–63. 1955; II. The American species of *Phyllanthus* described by Linnaeus. Jour. Arnold Arb. **37**: 1–14. 1956; III. A monographic study of the West Indian species of *Phyllanthus*. *Ibid.* **37**: 91–122, 217–268, 340–359. pls. 1–14. 1956; **38**: 51–80, 170–198, 295–373. pls. 15–23. 1957; **39**: 49–100, 111–212. pls. 24–32. 1958. [Includes several spp. of southeast. U. S.; extensive bibliography, **37**: 249–253.]
- . The origin of the cultivated *Xylophylla* hybrid, *Phyllanthus* × *elongatus*. Brittonia **11**: 177–182. 1959.
- . The species of *Phyllanthus* (Euphorbiaceae) collected by Sessé and Mociño. Sida **2**: 377–380. 1966. [Includes notes on *P. pentaphyllus*.]

## Subfam. EUPHORBIOIDEAE (Crotonoideae Pax)

## Tribe CROTONEAE Dumort., "Crotonieae"

Subtribe *Jatrophiae* Griseb., "Jatropheae"5. *Jatropha* Linnaeus, Sp. Pl. 2: 1006. 1753; Gen. Pl. ed. 5. 437. 1754.

Shrubs or small trees, or a few species herbaceous. Leaves alternate, stipulate (stipules often glandular), petioles short to longer than the blade, blades entire, toothed, or palmately lobed. Plants monoecious [rarely dioecious]; flowers in terminal, often long-stalked, dichasia, the lower flowers female, the distal ones male. Flowers with biseriate perianth; calyx synsepalous, 5-lobed, sepals imbricate or open in aestivation; petals 5, imbricate to contorted, free or coherent (but not truly connate). Male flower: disc [entire or] dissected; stamens 8–10, connate, anthers biver-ticellate; pollen globose, inaperturate, clavate; vestigial gynoecium absent. Female flower: disc cupular or pulviniform; carpels [2] 3 [rarely 4]; styles more or less connate at the base, bifid, the style-branches entire [bifid]; ovary glabrous or pubescent; ovules 1 in each locule, anatropous, nucellar beak conspicuous. Fruit capsular; mericarps crustaceous to woody; columella persistent. Seeds 1 in each locule, more or less ellip-soidal, testa crustaceous, carunculate; endosperm copious; embryo straight, cotyledons thin, broader and longer than the radicle. (Including *Aden-oropium* Pohl, *Curcas* Adans., *Mozinna* Ortega.) TYPE SPECIES: *J. gossypifolia* L.; see McVaugh, Bull. Torr. Bot. Club 71: 457. 1944. (Name from Greek, *iatros*, physician, and *phago*, to eat, in allusion to medicinal and edible properties of the seeds and roots.)

In the circumscription of Pax & Hoffmann and McVaugh, *Jatropha* includes 125–150 tropical species of very diverse habit; a majority (70–80) of these are American, but 40–50 occur in Africa. Because of the diversity within the genus and the confused concept held by Linnaeus and many subsequent workers, the literature is beset with both nomenclatural and taxonomic problems. Although *Cnidoscolus* has been retained within *Jatropha* as recently as the revision of 1910 by Pax, it is actually very distinct, as pointed out by McVaugh. Various segregate genera have been recognized by writers of local floras in the southeastern United States and elsewhere, but Miller & Webster have shown that there is no good evidence for doing so.

According to the treatment of McVaugh, the two Southeastern taxa of *Jatropha* belong to different sections. Representing sect. MACRANTHAE Pax, which is composed of species having a nonimbricate male calyx and glabrous reddish petals, is *J. multifida* L. This shrubby or arborescent species, easily recognized by its deeply divided leaves with 10 or more sharply toothed lobes, occurs from Mexico and the West Indies south to Brazil, and has been introduced into the Old World. Although no speci-mens have been seen, Small reported it from the Everglade Keys in Dade County, Florida, and it seems likely that the species may become exten-

sively naturalized in extreme southern Florida, as it is very commonly cultivated there.

Our other species, *Jatropha gossypifolia* L., has thus far been reported only from the island of Key West; but it seems probable that it, too, will become more widespread, at least in the Florida Keys, as it is extremely weedy in other areas of the Caribbean. It belongs (as type species) to sect. JATROPHA (§ *Adenorhopium* of McVaugh), a group characterized by having distinctly imbricate male calyx lobes, pubescent petals connivent into a short "tube," and seeds with prominently fimbriate caruncle. *Jatropha gossypifolia* is easily distinguished from its local congener, *J. multifida*, by means of its broadly and more shallowly lobed leaves beset with many stalked glands. The single specimen seen of *J. gossypifolia* from Key West would fit into var. *elegans* (Kl.) Muell. Arg. because of its glabrous leaves.

Miller and Webster have shown that five species of *Jatropha* investigated cytologically have  $2n = 22$ ; the species are then presumably diploid, with  $x = 11$ . More recently, Miller & Webster have reported two additional counts, one of which (for *J. dioica* Sessé) represents a tetraploid chromosome complement ( $2n = 44$ ). This cytological evidence strongly supports the taxonomic association of *Jatropha* with *Aleurites*, as proposed by Bentham, since the latter genus also has a base number of 11.

A number of other tropical species of *Jatropha* are cultivated in southern Florida and may be found as escapes. These include the very ornamental *J. integerrima* Jacq. (*J. hastata* Jacq., *J. pandurifolia* Andr.) with brilliant scarlet flowers; *J. Curcas* L., with yellowish-green flowers and somewhat fleshy fruits; and *J. podagrica* Hook., with succulent stems, peltate leaves, and small, red flowers.

Species of *Jatropha* are of some economic importance in the tropics, although not the basis for any major industry. The seeds of *J. Curcas* are valued for their purgative properties and for the oil which can be used in the manufacture of soap (Lanjouw, Wilbur). The seeds are dangerously poisonous when fresh, due to the presence of the alkaloid curcine; but when roasted they are edible and distinctly palatable. Other species, such as *J. multifida*, have seeds with somewhat similar properties.

#### REFERENCES:

- Under family references see ASSAILLY, BENTHAM, DEHAY, DEWILDEMAN, FROEMBLING, GAUCHER, INGRAM, MICHAELIS, MILLER & WEBSTER, PUNT, and SCOTT; under *Cnidoscolus* see McVAUGH (1943, 1944).
- HOLM, T. The seedlings of *Jatropha multifida* L. and *Persea gratissima* Gärtner. Bot. Gaz. 28: 60-64. 1899. [Describes the unusual seedling of *J. multifida* in which cotyledons remain inside seed coat.]
- MACKENZIE, K. K. Type of the genus *Jatropha*. Bull. Torrey Bot. Club 56: 213-215. 1929.
- McVAUGH, R. The jatrophas of Cervantes and of the Sessé and Mociño Herbarium. Bull. Torrey Bot. Club 72: 31-41. 1945.
- . The genus *Jatropha* in America; principal intrageneric groups. Bull. Torrey Bot. Club 72: 271-294. 1945.

- MILLER, K. I., & G. L. WEBSTER. Systematic position of *Cnidoscolus* and *Jatropha*. *Brittonia* 14: 174–180. 1962.
- POHL, J. E. *Plantarum Brasiliae. Icones et Descriptae.* vol. 1. xvi + 136 pp. *pls.* 1–100. Vindobonae. 1826–1828.
- RAO, A. R., & M. MALAVIYA. On the latex-cells and latex of *Jatropha*. *Proc. Indian Acad. Sci. B.* 60: 95–106. *pls.* 4, 5. 1964.
- WILBUR, R. L. A synopsis of *Jatropha*, subsection *Eucurcas*, with the description of two new species from Mexico. *Jour. Elisha Mitchell Sci. Soc.* 70: 92–101. 1954.

6. **Aleurites** G. Forster, *Char. Gen. Pl.* 111. *pl.* 56. 1776.

Deciduous [evergreen] trees; branches and leaves with indumentum of stellate and simple hairs. Leaves alternate, stipulate (but stipules caducous and mature leaves thus appearing exstipulate), long-petioled; blades entire or lobed, palmately veined, glandular at the base. Plants monoecious; flowers in terminal panicle-like cymes. Perianth biseriate: calyx calyptrate in bud, rupturing valvately into 2 or 3 lobes at anthesis; petals 5, large and showy, imbricate or contorted. Male flower: disc of 5 segments [entire]; stamens 8–10[–20], connate; anthers introrse [extrorse], dehiscent longitudinally; pollen globose, inaperturate, clavate; vestigial gynoecium absent. Female flower: disc dissected into 5 segments; carpels [2] 3–5; styles free, bifid; ovules 1 in each locule, anatropous. Fruit drupaceous, more or less tardily dehiscent. Seeds 1 in each locule, ecarunculate, testa thick and woody; endosperm copious, oily; embryo straight, cotyledons broad and palmately veined, much longer than the radicle. TYPE SPECIES: *A. triloba* G. Forst. = *A. moluccana* (L.) Willd. (Name from Greek, *aleurites*, floury, in allusion to the pale coating of pubescence on leaves and stems.) — CANDLE NUT, TUNG TREE.

A small but economically important genus of five or six species native to the Old World. The genus was widely separated from *Jatropha* in the treatment of Mueller but fairly closely associated with it by Bentham and by Pax. Evidence from cytological and palynological studies definitely favors the latter view (Erdtman, Miller & Webster).

In the southeastern United States *Aleurites Fordii* Hemsl., the tung oil tree, is extensively cultivated, and has become naturalized to a limited extent. Herbarium specimens have been seen from Florida and Louisiana, and Thorne has reported it from Georgia. The species belongs to sect. DRYANDRA (Thunb.) Muell. Arg., which comprises four eastern Asiatic species. The section is characterized by having an indumentum of bifurcate hairs, showy flowers with petals 1.5 cm. long or more, 3–5 carpels, and a more-or-less dehiscent fruit. *Aleurites Fordii*, the only deciduous species in the genus, is adapted to a more temperate climate than its congeners. It is native to forested regions in central and western China, extending as far north as Hupeh and Szechuan provinces. As grown in the United States, it is an ornamental tree in aspect somewhat resembling *Firmiana simplex* (L.) F. W. Wight (Sterculiaceae). The attractive



flowers, appearing in early spring before the leaves are expanded, are white with pink veins.

Despite its great current economic importance, the tung tree was long confused with the Japanese wood-oil tree (*A. cordata* (Thunb.) R. Br. ex Steud.) and the Mu-yu tree (*A. montana* (Lour.) Wilson), of southern China and Viet Nam. Both these species, however, are evergreen trees adapted to tropical climates and have wrinkled fruits, rather than the smooth ones of *A. Fordii*.

According to Newell *et al.*, tung oil trees were first planted in the southeastern United States in 1906, and since then they have become extensively cultivated in Mississippi, Alabama, Georgia, and northern Florida. The oil, which is contained in the endosperm of the seed, is a valuable drying oil which is essential for the manufacture of the best waterproof varnishes. The seeds have drastic purgative properties similar to species of *Jatropha* and can cause severe poisoning if eaten raw; the plant may therefore have minor medicinal uses in addition to its value to the paint industry.

All of the other species of *Aleurites* can be grown in southern Florida (from Palm Beach County southward), but they are not seriously cultivated on a commercial scale. *Aleurites moluccana* (L.) Willd., candle nut or kukui nut, is cultivated all around the tropics; it can be grown as far north as Brevard County and may quite possibly become naturalized to some extent. The type (and perhaps only) species in sect. ALEURITES, it differs from the species previously discussed in having an indumentum of stellate hairs, smaller flowers (petals usually less than 1 cm. long), and indehiscent fruits of only two carpels.<sup>10</sup> Cytological evidence provided by Stockar shows that *A. moluccana* is a tetraploid, with  $2n = 44$ , whereas the four species of sect. DRYANDRA are all diploids, with  $2n = 22$ .

Some interesting experimental taxonomy of *Aleurites* has been accomplished (more or less inadvertently) by tung-oil breeders who have crossed *A. Fordii* with other species in an effort to obtain cultivars with improved disease resistance or a delayed flowering period (and thus less chance of frost damage). Merrill and Kilby report that crosses can be made readily between *A. Fordii* and *A. montana*, but that the  $F_1$  hybrids are partially sterile. Unfortunately, most of their data involves the results of backcrosses, and neither they nor other workers have presented any sort of a

<sup>10</sup> Airy Shaw has recently proposed (Kew Bull. 20: 393-395. 1966) a narrow generic circumscription in which *Aleurites* would include only *A. moluccana* (and the probably synonymous *A. Remyi* Sherff), while *A. Fordii* and its relatives would be transferred to *Vernicia* Lour., and *A. trisperma* Blanco would belong to a new genus *Reutealis* Airy Shaw. If it were not for *A. trisperma*, a reasonable argument could be made for recognizing with generic status the taxonomic gap between the small-flowered, indehiscent-fruited *A. moluccana* and the larger-flowered, dehiscent-fruited species of more temperate areas. However, in flower size and indument, *A. trisperma* to some extent bridges the gap between the extremes within the genus; and all these species have in common similar leaves, calyptrate calyx, and large, ecarunculate, oily seeds. In my opinion, the propriety of these segregations must remain in doubt until the generic limits in this entire complex (including *Deutzianthus* Gagnep. et al.) are revised monographically.

summary of crossing results which would indicate the degree of reproductive incompatibility between the species.

#### REFERENCES:

- Under family references see AIRY SHAW (1966), BAILLON, DEHAY, GAGNEPAIN, GAUCHER, MÄDEL, MICHAELIS, PAX (1910, 1919), PERRY, POTBURY, PUNT, RITTERSHAUSEN, SMITH, THORNE, and WHEELER.
- ANGELO, E., R. T. BROWN, & H. J. AMMEN. Pollination studies with tung trees. *Proc. Am. Soc. Hort. Sci.* **41**: 176-180. 1942.
- BISWAS, K. Cultivation and systematic study of the tung oil yielding trees (*Aleurites*) in India. *Jour. Sci. Industr. Res.* **4**: 260-272. 1945.
- BLACKMON, G. H. Tung oil — a gift of China. *Econ. Bot.* **1**: 161-175. 1947. [General review of the industry.]
- BRAY, G. T. The cultivation and production of tung oil. I. *World Crops* **3**: 247-250. 1951.
- BROWN, R. T., & E. FISHER. Period of stigma receptivity in flowers of the tung tree. *Proc. Am. Soc. Hort. Sci.* **39**: 164-166. 1941.
- DICKEY, R. D., G. GILBERT, & C. M. GROPP. The genus *Aleurites* in Florida: I. Botanical characteristics; II. Chemical and physical properties of the oils. *Florida Agr. Exp. Sta. Bull.* **503**: 1-40. 1952.
- EMMEL, M. W. The toxic principle of *Aleurites Fordii* Hemsl. *Am. Veterin. Med. Assoc. Jour.* **103**: 162. 1943.\*
- . The toxic principle of the tung tree. *Florida Agr. Exp. Sta. Bull.* **431**: 1-35. 1947.
- FERNHOLZ, D. L. Cold resistance of buds, flowers and young fruits of tung. *Proc. Am. Soc. Hort. Sci.* **41**: 124-126. 1942.
- GOEZ, O. C. Cromosomos en *Aleurites moluccana* Willd. *Arq. Jard. Bot. Rio Janeiro* **7**: 5-10. 1947.
- GRANER, E. A. Notes on the chromosome number and morphology in root tips of tung (*Aleurites Fordii* Hemsl.). *Arch. Inst. Biol. Veg. Rio Janeiro* **2**: 81-82. *pl.* 1. 1935.
- HEMSLEY, W. B. *Aleurites Fordii*. *Hooker's Ic. Pl.* **29**: *pls.* 2801, 2802. 1906.
- . Revision of the synonymy of the species of *Aleurites*. *Bull. Misc. Inf. Kew* **1906**: 119-121. 1906.
- . The wood-oil trees of China and Japan. *Ibid.* **1914**: 1-4. 1914.
- HINKUL, S. G. Tungovoe derevo. (In Russian.) *Bull. Appl. Bot.* **2**: 137-153. 1935. [Discusses and illustrates distinctions between *A. cordata*, *A. Fordii*, and *A. montana*.]
- HOH, H. C. Genus *Aleurites* in Kwantung and Kwangsi. *Lingnan Sci. Jour.* **18**: 303-327, 513-524. *pls.* 17-21. 1939. [Provides a good key to 3 spp., original illustrations, and discusses distributions in S. China.]
- KLIMONO, K. Hybridization of the tung tree. *Soviet. Subtrop.* **5**: 87-90. 1937.\*
- LANGERON, M. Le genre *Aleurites* Forst. (Euphorbiacées): systématique-anatomie-pharmacologie. 160 pp. *4 pls.* Paris. 1902.
- LAYCOCK, D. H., & L. J. FOSTER. Rainfall and biennial bearing in tung (*Aleurites montana*). *Nature* **176**: 654. 1955.
- MCCANN, L. P. Development of the pistillate flower and structure of the fruit of tung (*Aleurites Fordii*). *Jour. Agr. Res.* **65**: 361-378. *4 pls.* 1941.
- . Embryology of the tung tree. *Ibid.* **71**: 215-229. 1945.
- , W. S. COOK, & C. R. CAMPBELL. Factors affecting time of initiation and

- rate of development of pistillate flowers of the tung tree. Proc. Am. Soc. Hort. Sci. 39: 157-160. 1941.
- MERRILL, S. Heterosis in tung. Proc. Am. Soc. Hort. Sci. 71: 231-236. 1958.
- & W. W. KILBY. Progress in hybridizing *Aleurites Fordii* with *A. montana*. Proc. Am. Soc. Hort. Sci. 78: 225-229. 1961.
- MOWRY, H. Variation in the tung-oil tree. Florida Agr. Exp. Sta. Tech. Bull. 247: 1-32. 1932.
- NEWELL, W., H. MOWRY, & R. M. BARNETTE. The tung-oil tree. Florida Agr. Exp. Sta. Bull. 280: 1-67. 1935.
- SELL, H. M., & F. A. JOHNSTON, JR. Biochemical changes in terminal tung buds during their expansion prior to blossoming. Pl. Physiol. 24: 744-752. 1949.
- SHERFF, E. E. Additional studies of the Hawaiian Euphorbiaceae. Field Mus. Publ. Bot. 17: 547-576. 1939. [Description of *A. Remyi* Sherff.]
- . Some additions to our knowledge of the flora of the Hawaiian Islands. Am. Jour. Bot. 31: 151-161. 1944. [Additional notes on *A. Remyi*.]
- STOCKAR, A. Complemento cromosómico diploide de algunas especies de *Aleurites*. Revista Argent. Agron. 13: 253-255. pl. 6. 1946. [Includes all spp.]
- . Comunicación preliminar sobre hibridaciones entre varias especies de *Aleurites*. Ibid. 14: 33-38. 1947.
- WARD, F. K. A hybrid *Aleurites*. Gard. Chron. III. 122: 128-129. 1947. [*A. montana* × *A. Fordii*; no quantitative data.]
- WEBSTER, C. C. A note on pollination in budded plantations of tung trees (*Aleurites montana*). Nyasaland Agr. Quart. Jour. 3: 17-19. 1943.\*
- . Observations and experiments on flowering and pollination of the tung tree. E. Afr. Agr. Jour. 9: 136-143. 1944.\*
- WHEELER, L. C. Notes on the genus *Aleurites*. Harvard Univ. Bot. Mus. Leaflet 7: 119-122. 1939. [Largely details of nomenclature.]
- WILSON, E. H. The "wood-oil" trees of China and Japan. Bull. Imp. Inst. London 11: 441-461. 1913. [The first clear discrimination of *A. montana*.]
- WIT, F. Het botanisch onderzoek van *Aleurites*. Landbouw Nederl. Indië 15: 9-27. 1939.

Subtribe *Manihotinae* Muell. Arg., "Manihoteae"

7. *Manihot* Miller, Gard. Dict. Abr. ed. 4. 1754.

Herbs or shrubs [rarely trees], often with tuberous roots, stems laticiferous. Leaves alternate, stipulate (stipules often very small), long-petioled; blades mostly palmately lobed, stipellate at the base but without distinct foliar glands. Plants monoecious; flowers in terminal, sometimes pseudo-axillary panicles, the female flowers on several lateral basal axes, the male flowers more or less racemose along the central axis. Perianth uniseriate (presumably petals missing), often petaloid; calyx lobes imbricate. Male flower: calyx synsepalous, more or less cyathiform; disc central, intrastaminal, 5-lobed, lobes more or less bifid; stamens 10, free, biseriate, the outer opposite the calyx-lobes; anthers introrse, dehiscing longitudinally; pollen globose, periporate, exine clavate; rudimentary gynoecium present or absent. Female flower: calyx synsepalous but more deeply lobed than the male; disc pulviniform, staminodia sometimes present as well; carpels 3; styles 3, connate below; stigmas dilated and lacer-

ate or multifid; ovules 1 in each locule, anatropous. Fruit capsular, dehiscent, sometimes winged; columella dilated above, often persistent. Seeds smooth, carunculate; seed coats thin and crustaceous; endosperm starchy; embryo with broad palmately veined cotyledons. LECTOTYPE SPECIES: *Jatropha Manihot* L. = *Manihot esculenta* Crantz; see Adanson, Fam. Pl. 2: 356. 1763. (Name from *manioc*, aboriginal Indian word for the cassava plant.) — CASSAVA, TAPIOCA PLANT.

Over 150 species of *Manihot* are known, according to Pax and Hoffmann; the number may, however, prove to be considerably smaller than this when the genus is monographically revised. The majority of the species is native to Brazil, but a respectable concentration is present in Mexico, and two or three cross the border into the United States.

Although originally confounded with species of *Jatropha* by Linnaeus, *Manihot* is very distinct by virtue of its apetalous flowers, central male disc, and periporate pollen grains. The basic chromosome number of  $n = 18$  ( $x$  probably = 9) rather than  $x = 11$  in *Jatropha* also supports a rather wide taxonomic separation. Mueller's placement of the two genera in adjacent subtribes presents a reasonable picture of their affinity. As pointed out by Miller & Webster, the closest genus to *Manihot* appears to be *Cnidoscolus* (*q.v.*).

The tapioca plant, *Manihot esculenta* Crantz (*M. utilissima* Pohl), is cultivated in southern Florida, as elsewhere in the Caribbean area, and has been reported by Small (as *Jatropha Manihot* L.) to be naturalized in the Florida and Everglade Keys. Lakela & Craighead report it from Collier, Dade, and Monroe counties. One specimen (Small, Nov. 1904) from Dade County does seem to represent this species, so that the above records may well be correct. However, collections of naturalized *Manihot* north of extreme southern Florida probably do not represent the cassava plant, which is not sufficiently frost-resistant to overwinter in northern Florida. The record of *M. esculenta* cited by Thorne from Georgia is erroneous. His collection (Thorne 5866), as well as naturalized plants from northern Florida (e.g., Godfrey 54844), may tentatively be identified as *M. Grahamii* Hook. (*M. Tweedieana* Muell. Arg.), a species native to Paraguay and western Brazil.<sup>11</sup> The somewhat notched leaflets of these collections suggest *M. carthaginensis* (Jacq.) Muell. Arg., and at least one sheet has been so identified. However, that species has much smaller stipules, and the leaflets are distinctly lyrate-lobed.

According to the classification of Pax, both of these naturalized species belong to sect. PARVIBRACTEATAE Pax, which includes about 35 to 40 mainly Brazilian species characterized by deeply lobed leaves and small, inconspicuous bracts. *Manihot Grahamii*, assigned to subsect. ELATAE Pax, may be recognized by its slender, attenuate-acuminate, laterally toothed stipules which become 1 cm. or more long, its large glabrous male

<sup>11</sup> Croizat (1943) has reduced *M. Grahamii* to a synonym of *M. flabellifolia* Pohl, and he may be correct in doing so. However, the long, glabrous, toothed stipules and completely glabrous male calyx of the Georgia and Florida plants do not accord with Mueller's description of Pohl's species.

calyces (mostly 12–15 mm. long), thin leaves with (5–)7–10 abruptly acuminate lobes, and wingless capsules with relatively large seeds (7 mm. or more across). The true cassava plant, *M. esculenta*, belongs to subsect. UTILISSIMAE Pax because of its internally pubescent male calyx and deeply lobed leaves. It may be distinguished from *M. Grahamii* by its shorter stipules, smaller male calyces (less than 10 mm. long), thicker leaves with fewer (3–7) lobes which are gradually acuminate and paler beneath, and its distinctly wing-angled capsules with somewhat smaller seeds (mostly 6.5 mm. or less across).

Cytological studies on eight species of *Manihot* have demonstrated a uniform chromosome number of  $2n = 36$ , except that one accession of *M. esculenta* was tetraploid ( $2n = 72$ ). Actually, the genus may be basically tetraploid, since  $x = 9$ , in all probability. As pointed out by Miller & Webster, the cytological evidence alone suggests that *Manihot* is more closely related to *Cnidoscolus*, which also has  $x = 9$ , than to *Jatropha*, in which  $x = 11$ . Except for *Cnidoscolus*, *Manihot* does not appear to have any close relatives, and these two genera would appear to be the sole members of subtribe Manihotinae.

*Manihot esculenta* is a plant of great economic importance as a carbohydrate source in lowland tropical areas. Although cassava is most important as a starchy food in Latin America, it is also cultivated fairly intensively in Africa and to some extent in Asia as well. Despite the importance of the crop, the taxonomy of the cassava plant and closely related species is surprisingly imperfect. Rogers has shown that there is no morphological correlation between the two major "convariants" of manioc defined on root and stem characters with the "sweet" or "sour" nature of the roots. In sweet cultivars, the hydrocyanic acid is confined to the phelloderm of the root, but in the sour cultivars it occurs in the cortex as well, and the root is consequently dangerously poisonous unless boiled and mashed or strained. Rogers notes that sweet cultivars are found mainly west of the Andes and bitter to the east, and suggests that possibly cultivation began on the eastern slopes of the Andes.

Although of little present importance, arborescent species of *Manihot* were at one time an important source of rubber (Zimmermann, Polhamus). The most valuable species appears to have been the Ceará rubber tree, *M. Glaziovii* Muell. Arg., of sect. GLAZIOVIANAE Pax, which was extensively planted in East Africa prior to World War I. *Manihot dichotoma* Ule was also planted in Africa to a considerable extent. Although plants of *Manihot* could be cultivated in drier regions than *Hevea*, greater difficulty in tapping and obtaining high yields led to its drop from favor.

Because of the low protein content in cassava starch, it is an inferior carbohydrate source and a potential cause of malnutrition in areas where it is used heavily; consequently, efforts have been made to develop cultivars with enriched roots by crossing with other species (Bolhuis). These crossing programs, although purely utilitarian, are beginning to yield interesting data with regard to species relationships within *Manihot*, as noted by Rogers. Such species as the Guianian *M. saxicola* Lanj. and *M.*

*melanobasis* Muell. Arg. are easily crossed with *M. esculenta*; according to Bolhuis and Jennings, they may not even be distinct species. This evidence suggests that the taxonomic arrangement of Mueller, which was followed in general by Pax, in 1910, may be quite artificial, and that the infrageneric taxa of *Manihot* may have to be drastically revised.

## REFERENCES:

- Under family references see DEHAY, GAUCHER, HERBERT, INGRAM, LAKELA & CRAIGHEAD, LANJOUW, MCVAUGH, MICHAELIS, MUELLER (1874), PAX & HOFFMANN (1910, II), PERRY, POLHAMUS, PUNT, SCHWEIGER, SCOTT, THORNE, VENTURA (1940), DE WILDEMAN, and WILLIAMS. Under *Jatropha* see MACKENZIE.
- ABRAHAM, A. Natural and artificial polyploids in tapioca (*Manihot utilissima*). Proc. 31st Indian Sci. Congr. 1944(3): 73. 1945?
- BIANCHINI, M. La geografia della manioca. Boll. Soc. Geogr. Ital. VIII. 4: 26-53. 1951. [Mostly economic, but with extensive bibliography.]
- BOLHUIS, G. G. A survey of some attempts to breed cassava-varieties with a high content of proteins in the roots. Euphytica 2: 107-112. 1953. [Describes crosses between *M. esculenta* and *M. saxicola*.]
- CAPINPIN, J. M., & V. C. BRUCE. Floral biology and cytology of *Manihot utilissima*. Philip. Agr. 39: 306-316. 1955.
- CHANDRARATNA, M. F., & K. D. S. S. NANAYAKKARA. Studies in cassava. I. A classification of races occurring in Ceylon. Trop. Agr. Ceylon 101: 3-12, 214-222. 1945; II. Production of hybrids. *Ibid.* 104: 59-74. 1948.
- CIFERRI, R. Saggio di classificazione delle razze di Manioca (*Manihot esculenta* Crantz). Relaz. Monogr. Agrar.-Colon. 44: 1-58. 1938.\*
- . Fondamenti per una classificazione subspecifica della *Manihot esculenta* Crantz. Arch. Bot. Forlì 18: 27-33. 1942.\*
- COURS, G. Le manioc à Madagascar. Mém. Inst. Sci. Madagascar B. 3: 203-400. pls. 1-15. 1951. [Includes morphological notes, 207-273; results of interspecific crosses, 363-365.]
- CROIZAT, L. A study of *Manihot* in North America. Jour. Arnold Arb. 23: 216-225. 1942. [Discussion and description of new spp., but not a full revision.]
- . Preliminari per uno studio del genere "Manihot" nell'America meridionale. Revista Argent. Agron. 10: 213-226. 1943. [Listing, without keys; combines *M. Grahamii* and *M. Tweedieana* with *M. flabellifolia*.]
- . *Manihot Tweedieana* Mueller is unacceptable. *Ibid.* 11: 173, 174. 1944. [Correctly points out priority of *M. Grahamii*.]
- GRANER, E. A. Genetica de manihot. I. Hereditarietà da forma da folha e da coloração da película externa das raízes em *Manihot utilissima* Pohl. Bragantia 2: 13-22. 1942.
- HOOKE, W. J. *Manihot Grahamii*. Hooker's Ic. Pl. 6: pl. 530. 1843.
- JENNINGS, D. L. Further studies in breeding cassava for virus resistance. E. Afr. Agr. Jour. 22: 213-219. 1957.
- . *Manihot melanobasis* Muell. Arg. — a useful parent for cassava breeding. Euphytica 8: 157-162. 1959.
- LANJOUW, J. Two interesting species of *Manihot* L. from Suriname. Rec. Trav. Bot. Néerl. 36: 543-549. pl. 9. 1940. [*M. saxicola* Lanj., new sp.]
- NICHOLS, R. F. W. Breeding cassava for virus resistance. E. Afr. Agr. Jour. 12: 184-194. 1947.
- PAX, F. Euphorbiaceae-Crotonoideae-Adrianeae. Pflanzenreich IV. 147-II(Heft 44): 1-111. 1910. [*Manihot*, 21-99.]

- ROGERS, D. J. Intraspecific categories of *Manihot esculenta*. *Science* 126: 1234, 1235. 1957.
- . Studies on *Manihot esculenta* Crantz and related species. *Bull. Torrey Bot. Club* 90: 43–54. 1963.
- . Some botanical and ethnological considerations of *Manihot esculenta*. *Econ. Bot.* 19: 369–377. 1965. [Includes speculations as to interspecific relationships, as well as place of origin of cassava.]
- SCHERY, R. W. Manioc — a tropical staff of life. *Econ. Bot.* 1: 20–25. 1947.
- SCOTT, D. H. On the laticiferous tissue of *Manihot Glaziovii* (the Ceará rubber). *Quart. Jour. Microscop. Sci.* 24: 194–204. 1884.
- SENARATNA, J. E. Bisexual flowers in the manioc, *Manihot esculenta* Crantz (*M. utilissima* Pohl). *Ceylon Jour. Sci. A.* 12: 169. 1945.
- TOLEDO, A. P. Anatomia e desenvolvimento ontogenético da flor de mandioca. *Bragantia* 22: 465–476. 1963.
- . Anatomia e desenvolvimento ontogenético do fruto e da semente de mandioca. (English summary.) *Ibid.* 22: lxxi–lxxvi. 1964.
- TRACY, S. M. Cassava. U. S. Dep. Agr. Farmer's Bull. 167: 1–31. 1903.
- VIÉGAS, A. P. Anatomia da parte vegetativa da mandioca. *Inst. Agron. São Paulo Bol. Téc.* 74: 1–32. 1940.
- ZIMMERMANN, A. *Der Manihot-Kautschuk*. xli + 342 pp. Jena. 1913. [Description of rubber industry based on *M. Glaziovii* and related spp.]

8. *Cnidoscolus* Pohl, *Pl. Brasil. Ic. Descr.* 1: 56. 1827, nom. cons. prop.

Herbs, shrubs, or trees; stems and leaves containing milky latex and armed with stinging hairs; pith septate. Leaves palmately [or pinnately] veined or lobed [sometimes parted into segments and almost compound]; petioles usually long, glandular at junction with blade; stipules entire to laciniate [rarely obsolete]. Plants monoecious; flowers in terminal (sometimes pseudo-axillary) dichasia, the female flowers at the lower (proximal) nodes, male at the upper (distal) nodes. Flowers apetalous; calyx more or less petaloid, usually white. Male flower: calyx synsepalous; calyx lobes imbricate; disc annular; stamens 8–10[–25], the outer free and inner connate [or all connate]; pollen globose, periporate, clavate; staminal column without terminal filiform staminodia [these present in some exotic taxa]. Female flower: calyx aposepalous; sepals deciduous [synsepalous in some species]; disc annular, sometimes associated with staminodia; carpels 3 [rarely 5]; styles more or less free, several times bifid or laciniate [rarely once bifid], sometimes apically dilated; ovule 1 in each locule, anatropous. Fruit capsular [rarely drupaceous]; columella slender; Seeds 1 in each locule, carunculate; endosperm starchy; embryo straight, with broad cotyledons longer than the radicle. (*Bivonea* Raf.) LECTOTYPE SPECIES: *C. hamosus* Pohl; see Small in Britton and Brown, *Illus. Fl. No. U. S. ed. 2.* 2: 462. 1913. (Name most appropriately derived from Greek, *cnide*, nettle, and *skolos*, thorn, in allusion to the stinging properties of the plants.) — STINGING NETTLE, BULL-NETTLE.

This distinctive genus of about 50 American species has long been confused with *Jatropha*, due to the influence of Mueller, who so treated it. However, McVaugh (1944) pointed out its distinguishing characteristics

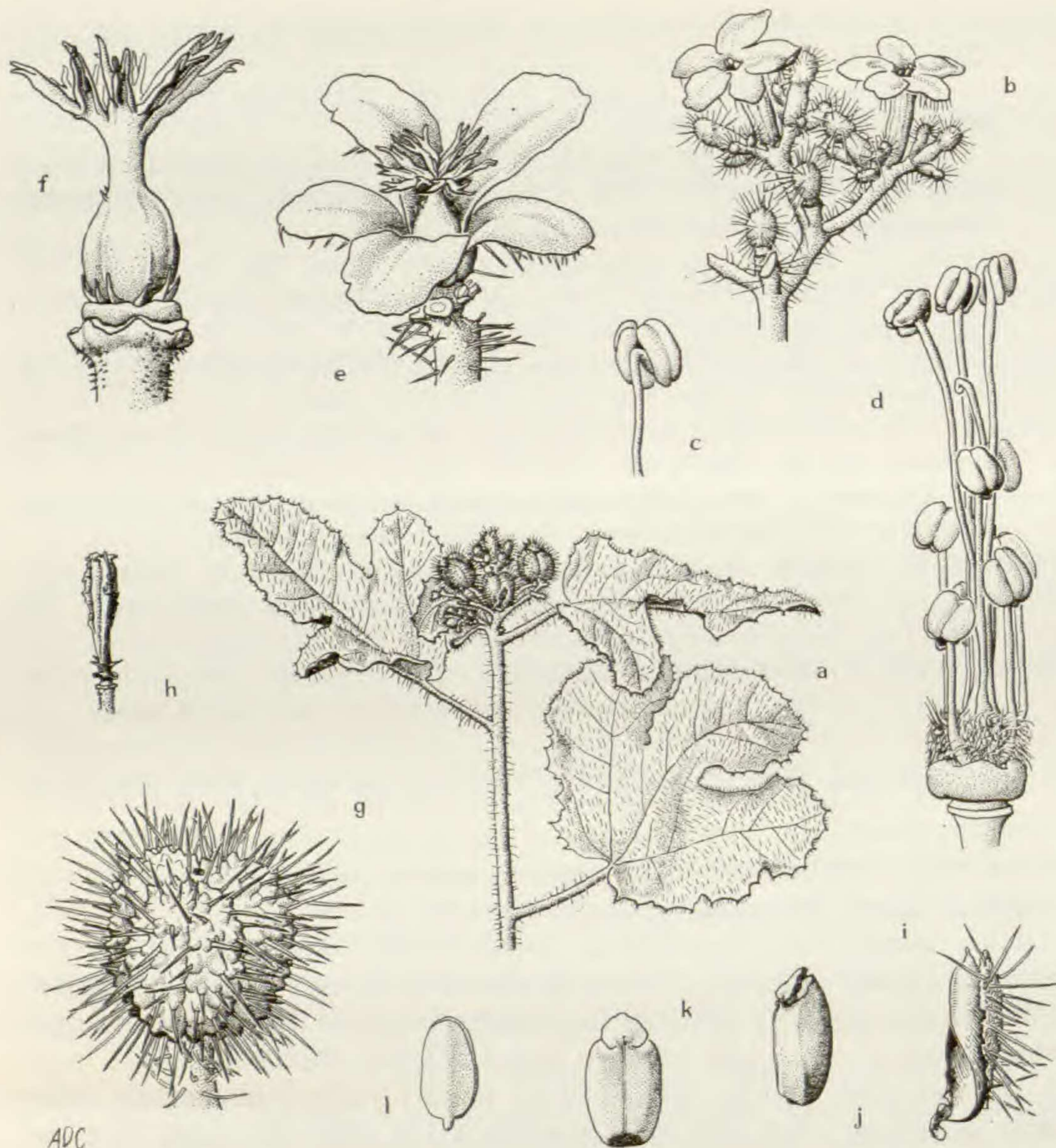


FIG. 1. *Cnidoscolus*. a-l, *C. stimulosus*: a, portion of flowering and fruiting plant,  $\times \frac{1}{2}$ ; b, part of cymose inflorescence with two young fruits, two male flowers, and buds,  $\times 1$ ; c, stamen from unopened bud to show attachment of anther,  $\times 6$ ; d, androecium after anthesis, showing disc, ten stamens, and staminode,  $\times 6$ ; e, female flower, with adjacent male buds removed — note quincuncial aestivation,  $\times 6$ ; f, gynoecium with disc and staminodia,  $\times 6$ ; g, nearly mature fruit,  $\times 2$ ; h, columella after dehiscence of schizocarp,  $\times 2$ ; **i, one valve of schizocarp after dehiscence, showing bony endocarp,  $\times 2$** ; j, k, lateral and adaxial surfaces of seed with caruncle,  $\times 2$ ; l, embryo,  $\times 2$ .

and correctly insisted that it is very distinct from *Jatropha*. Miller & Webster subsequently showed that evidence from petiolar anatomy, pollen morphology and chromosome counts agrees and furthermore suggests that *Cnidoscolus* is much more closely related to *Manihot*. Baillon long ago noted this relationship which has been generally ignored by later workers.

*Cnidoscolus* clearly differs from *Jatropha* in its uniseriate perianth, stinging hairs, petiolar glands, laciniate style tips, septate pith, and other



characters (McVaugh). Baillon noted that, although *Cnidoscolus* was much closer to *Manihot*, it differed in its free stamens and extrastaminal disc. The interesting South American *C. urnigerus* (Pax) Pax appears to be partly transitional between the two genera, since it has free stamens as in *Manihot* but the extrastaminal disc and stinging hairs of *Cnidoscolus*. There can now be little doubt that *Cnidoscolus* is more closely related to *Manihot* than to any other genus in the family, as is indicated in this treatment by the association of the two genera in the subtribe Manihotinae.

In our area *Cnidoscolus* is represented by two species belonging to sect. JUSSIEUIA (Houst.) Pax, which, in the circumscription proposed by McVaugh, is characterized by distinct outer filaments (but see *C. texanus*) and small multiple petiolar glands. Our representatives belong to the subsect. URENTES (Pax) Pax & Hoffm., a small group of five more or less herbaceous species which have the inner stamens united, and styles 2–3 times bifid. The only other representative of sect. JUSSIEUIA, the aberrant *C. urnigerus*, differs strongly in its completely distinct filaments and simply bifid styles, and perhaps should be referred to a different section. *Cnidoscolus stimulosus* (Michx.) Engelm. & Gray is widespread in dry, often sandy areas along the Coastal Plain from southeastern Virginia to the Florida Keys and west to Mississippi and eastern Louisiana; it is not recorded west of the Mississippi River in Louisiana. It may be recognized by its small male flowers (tube under 1 cm. long) with glabrous tube and small seeds (under 9 mm. long). Our other species, *Cnidoscolus texanus* (Muell. Arg.) Small, differs in being a much coarser and more viciously stinging plant with larger stipules, male flowers (tube 1–2 cm. or more, spinose), and seeds (mostly 12–15 mm. long). The androecium of *C. texanus* also differs in having the outer whorl of stamens connate below, so that the species does not agree with the sectional character. It is a characteristically Texan species of limestone areas, but it enters our range in southwestern Arkansas and western Louisiana. A gap of about 150 miles separates its easternmost station in Rapides Parish, Louisiana, from the westernmost known locality of *C. stimulosus* in Washington Parish. The two species are “classical” vicariants, therefore, and may represent the collateral descendants of a widespread ancestral population on the pre-Pleistocene coastal plain.

Cytological observations (Miller & Webster) indicate a chromosome number of  $2n = 36$  in both local species, suggesting that they are tetraploid if  $x = 9$ . The same chromosome number has been reported for four Mexican species (Miller & Webster), so the genus is cytologically homogeneous so far as is known, and its karyotype appears close to that of *Manihot*.

The relationships between our two species and the other taxa of sect. JUSSIEUIA remain to be worked out. Mueller included all of the taxa of subsect. URENTES except *C. texanus* in his inclusive *Jatropha urens*.<sup>12</sup> As

<sup>12</sup> A complicating factor in the taxonomy of the *C. urens* group is the typification of *C. urens* (L.) Arthur. Mueller (1866) correctly pointed out that the specimen in the Linnaean Herbarium is not the common weedy plant but rather a very different

noted by McVaugh, however, both *C. stimulosus* and *C. texanus* seem to be sufficiently distinct species, whatever the disposition of the Brazilian taxa of the complex.

It is perhaps not too surprising, in view of its relationship with *Hevea* and *Manihot*, that *Cnidoscolus* also includes species with a high rubber content in the latex. At least two arborescent Mexican species, *C. elasticus* Lundell and *C. tepiquensis* (Cost. & Gall.) Lundell, the "chilte rojo" and "chilte blanco" of Mexicans, yield rubber somewhat resembling that of *Hevea* (McVaugh, Lundell). During World War II these were investigated as possible emergency sources of rubber, but the latex proved to have too high a resin content, and no commercial production of any importance was sustained. Since the war, some commercial exploitation has continued, for the latex provides a useful additive to other gutta-like gums (Williams).

The characteristic stinging hairs of *Cnidoscolus* have never been intensively studied, although Solereder and Lutz mentioned their resemblance to those of *Urtica*. The mechanism may be similar, as in both genera the unicellular hairs end in a minute spherical tip which breaks off to permit injection of the poison. In *Cnidoscolus* the size of the hairs and their distribution on parts of the plant, especially the flowers, varies considerably, although the fruit is usually quite spiny, even if the perianth is not. A few tropical species, especially *C. aconitifolius* (Mill.) Johnston and *C. chayamansa* McVaugh, have nearly unarmed leaves which are used as a vegetable and may prove to be a good source of vitamin C.

#### REFERENCES:

- Under family references see BAILLON, DEHAY, GAUCHER, INGRAM, HERBERT, LOURTEIG & O'DONELL (1943), MILLER & WEBSTER, PAX & HOFFMANN (1910, I), POLHAMUS, PUNT, SOLEREDER, and UPHOF.
- BONDAR, G. Peñão, *Cnidoscolus Marcgravii* Pohl, novo recurso oleifero da Bahia. Inst. Centr. Fomento Econ. Bahia Bol. 12: 1-16. pls. 1-4. 1942.
- CROIZAT, L. New and critical Euphorbiaceae of Brazil. Trop. Woods 76: 11-14. 1943. [Mainly on *Cnidoscolus*; discusses nature of the perianth.]
- JOHNSON, P. R. Texas bullnettle and its control. Bull. Tex. Agr. Exp. Sta. 1052: 1-11. 1966. [Includes descriptions and illustrations of underground parts of *C. texanus*.]
- LEÓN, HNO. *Cnidoscolus* y *Victorinia* gen. nov. en Cuba y Española. Mem. Soc. Cuba. Hist. Nat. 15: 235-244. pls. 23, 24. 1941. [Describes new genus on basis of 2 Greater Antillean spp. with 5 carpels and drupaceous fruit.]
- LUNDELL, C. L. *Cnidoscolus elasticus*, the source of highland chilte, a remarkable new rubber yielding tree from the states of Durango and Sinaloa, Mexico. Field Lab. 12: 33-38. 1944.

species belonging to sect. CALYPTROSOLEN (i.e., *C. Kunthianus* (Muell. Arg.) Pax & Hoffm.). This specimen is so different, however, from the illustrations of Commelin, Marcgrav, and Plukenet cited by Linnaeus that it is hardly desirable to designate it as the type. The Commelin illustration accords rather well with the plant later described by Pohl as *C. Marcgravii*, so that it may perhaps serve to typify the species. In that event, *C. urens* (*sensu stricto*) is to be interpreted as a Brazilian plant similar to *C. stimulosus*, but differing, *inter alia*, in its closely pubescent leaves and differently shaped seeds (more compressed, notched at the base, and with a smaller caruncle).

- . The genus *Cnidoscolus* in Mexico: new species and critical notes. Bull. Torrey Bot. Club 72: 319–334. 1945.
- LUTZ, O. The poisonous nature of the stinging hairs of *Jatropha urens*. Science 40: 609, 610. 1914. [Anecdotal; toxic principle not identified.]
- McVAUGH, R. The Mexican species of *Jatropha* (with special reference to possible sources of "chilte" rubber). 23 pp. Rubber Development Corp., Wash., D. C. 1943. [Primarily on spp. of *Cnidoscolus*, including a key and illustrations.]
- . The genus *Cnidoscolus*: generic limits and intrageneric groups. Bull. Torrey Bot. Club 71: 457–474. 1944.
- MENAU, P. A chemical analysis of *Jatropha stimulosa*. Jour. Agr. Res. 26: 259, 260. 1923. [Seeds contain ca. 51% fat, yielding oil similar to castor oil.]
- MILLER, K. I., & G. L. WEBSTER. Systematic position of *Cnidoscolus* and *Jatropha*. Brittonia 14: 174–180. 1962.
- PAX, F. Euphorbiaceae–Jatropheae. Pflanzenreich IV. 147(Heft 42): 1–148. 1910.
- SEIGLER, D. S., & J. J. BLOOMFIELD. The chemistry of the genus *Cnidoscolus* — I. The fatty acid components of the seed oil. Phytochemistry 6: 451. 1967. [Contains 71% linoleic acid.]
- WHEELER, L. C. *Pedilanthus* and *Cnidoscolus* proposed for conservation. Contr. Gray Herb. 124: 47–52. 1939.
- WILLIAMS, L. Laticiferous plants of economic importance. II. Mexican chilte (*Cnidoscolus*): a source of gutta-like material. Econ. Bot. 16: 53–70. 1962.

Subtribe *Crotoninae* Benth., "Eucrotoneae"

9. *Croton* Linnaeus, Sp. Pl. 2: 1004. 1753; Gen. Pl. ed. 5. 436. 1754.

Herbs, shrubs [or trees]; stems often with colored or resinous sap but not with milky latex; indumentum at least in part of branched or lepidote trichomes. Leaves alternate, sometimes crowded and subopposite or pseudo-whorled, stipulate (stipules sometimes obsolete), pinnately or palmately veined or sometimes lobed; petioles sometimes with distinct glands at junction with blade. Plants monoecious or (in a minority of species) dioecious; flowers in usually bisexual spiciform racemes or thyrses, the female flowers solitary at lower (proximal) nodes, the male flowers 1 to several at upper nodes. Flowers with biseriate or uniseriate perianth: petals usually present in male flowers, reduced or absent in female flowers. Male flower: calyx 5-lobed (lobes rarely 4 or 6), lobes imbricate to valvate; disc entire or dissected into segments alternate with the petals; petals isomerous with calyx lobes, mostly about as long (rarely absent); stamens [3–]8–20[–400], free, filaments usually inflexed in bud; anthers extrorse in bud; pollen globose, inaperturate, clavate; vestigial gynoecium absent; receptacle often densely lanate. Female flower: calyx lobes (4) 5–7(–10), sometimes accrescent; disc annular or rarely dissected, sometimes with staminodia; carpels 3 (rarely 2); styles free or nearly so, once to several times bifid or bipartite into slender tips; ovules 1 in each locule, anatropous, nucellus elongated into a slender beak. Fruit capsular [rarely somewhat fleshy]; columella persistent, usually slender;

seeds 1 in each locule, terete to compressed, carunculate; testa smooth and dry, usually thin; endosperm copious; embryo straight, cotyledons broader than and as long as or longer than the radicle. LECTOTYPE SPECIES: *C. aromaticus* L.; chosen here.<sup>13</sup> (Name from Greek, *kroton*, tick, in allusion to the resemblance of the seed of *Ricinus* to the arachnid; arbitrarily applied to the present genus by Linnaeus to replace Tournefort's *Ricinoides*).

A very large genus comprising more than 600 species, according to Pax & Hoffmann, or around 1000 species, in the opinion of Croizat. It seems probable that the latter estimate will prove to be somewhat inflated when the genus is monographically revised. More than two-thirds of the species are American, and, of these, the majority are South American and West Indian; perhaps 75 or 80 species occur in mainland North America.

In the circumscription established by Mueller and followed by later workers, *Croton* is a very natural and rather isolated genus, without any close relatives other than such small satellite genera as *Crotonopsis* and *Eremocarpus*.<sup>14</sup> The characteristic large pollen grains with large, hexagonally arranged excrescences are much like those in other subtribes of the tribe Crotonaeae. However, *Croton* is well characterized by the distinctive racemiform inflorescence and the male flowers with stamens inflexed in the bud. Furthermore, the stellate or lepidote pubescence and the non-milky sap of *Croton* permit its easy distinction from many other taxa of Crotonoideae.

The circumscription of the infrageneric taxa of *Croton* is as controversial as that of the genus is not. Bentham and various later workers sharply criticized the system of Mueller as highly artificial and unnatural; but it is most difficult to find clear-cut assemblages of species, and protracted acquaintance with the genus tends to induce greater sympathy for Mueller's adoption of an artificial arrangement. Johnston has sensibly placed the Texas species of *Croton* in informal groups, and Ferguson did not use any subgeneric designations at all. In the present treatment an attempt has been made to incorporate the results of recent anatomical and cytological investigations without introducing any more taxonomic changes than are absolutely necessary.

<sup>13</sup> Small (in Britton and Brown, *Illus. Fl. No. U. S.* ed. 2, 2: 454. 1913) selected *Croton Tiglium* L. as the type species, and he has been followed by recent workers. However, Klotzsch long ago removed that species as the type of a segregate genus *Tiglium*, and Baillon preserved Klotzsch's group as a section, while restricting sect. *Eucroton* to species with a valvate male calyx. The only species originally included in *Croton* by Linnaeus which have not been removed are *C. lacciferus* and *C. aromaticus*, so it would appear that one of these must be designated the lectotype. Since Geiseler combined the two species under the latter name, that one is chosen here.

<sup>14</sup> In agreement with the opinion of Macbride (*Publ. Field Mus. Bot.* 13(3A): 57. 1951), *Croton* is here construed to include *Julocroton* Mart. (*Beibl. Flora* 1837(2): 119. 1837). Despite the arguments of Croizat, *Julocroton* does not seem to be any more distinct than many other infrageneric groups of *Croton*, and it seems best treated as *Croton* sect. **Julocroton** (Mart.) Webster, comb. nov. No species of this section have as yet been reported from our area, although *C. argenteus* L. enters southern Texas and may possibly become established in peninsular Florida.

The 13 or 14 species of *Croton* in our area belong to seven sections. Section ANDRICHNIA Baill. (§ *Eluteria* Griseb.), the only section in which female flowers with well-developed petals occur, is represented by the interesting and rare *C. alabamensis* E. A. Sm. ex Chapm., which is known only from two populations occupying less than 100 acres in central Alabama (Bibb and Tuscaloosa counties). Farmer carefully studied the life history of the species, the reproductive biology of which is now the best known of any species of *Croton*. He found the Bibb County plants to be diploids ( $2n = 32$ ), whereas the larger-leaved plants from the Warrior River area, in Tuscaloosa County, are tetraploids ( $2n = 64$ ). The species does not appear to have any close relatives in North America, unless Croizat was correct in suggesting that *C. argyranthemus* is a depauperate member of this section.

Section CROTON, although by far the largest subgeneric group in the Muellerman sense (with over two-thirds of the species), is represented in our area by only three species. Plants of this section, which includes the "typical" crotons with smooth seeds, pubescent male receptacle, and pentamerous regular calyces, may be assigned to several subsections. Plants with stellate, rather than lepidote, indumentum and stamens relatively few in number (20 or less) belong in subsect. MEDEA (Kl.) Pax; our representatives are *C. linearis* Jacq. and *C. humilis* L., both tropical species confined to southern Florida. Subsection ARGYROCROTON Muell. Arg., including plants with lepidote indumentum, is represented by *C. argyranthemus* Michx., which occurs along the Coastal Plain from Georgia and Florida west into eastern and southern Texas.

Section ASTRAEA (Kl.) Baill. is in many ways the most distinctive group within *Croton* and has the best claims to generic status.<sup>15</sup> It is an entirely American group of less than 10 species, all of which except the local one, *C. lobatus* L., are confined to South America. *Croton lobatus* appears to be a newcomer to our flora, since it was first reported in 1965 by Lakela and Craighead from Dade County, Florida. It may be easily distinguished from other local species of *Croton* by its three-to-five-lobed leaves, glabrous male petals and receptacle, and cylindrical seeds. Despite the undoubted distinctiveness of *Astraea*, its species resemble some of those in the following section, and, except for the absence of oil cells mentioned by Froembling, there really seems to be no basis for excluding the group from *Croton*.

Section GEISELERIA (Kl.) Baill. (§ *Decarinium* of Mueller) is an entirely American group of about 30 species brought together by Mueller on the basis of the irregular female calyx which has two of the lobes greatly reduced. As Mueller himself admitted, the section may be unnatural; the species with lepidote leaves placed in series LAMPROCROTON Muell. Arg. should perhaps be referred to one or more other sections. Series GEISELERIA

<sup>15</sup> Mueller's circumscription of sect. ASTRAEA was arbitrarily based on the single character of the male receptacle, and is consequently unnatural. However, if the two North American species (*C. humilis* and *C. panduriformis*) are excluded, the remainder of the section represents a very natural and distinctive group.

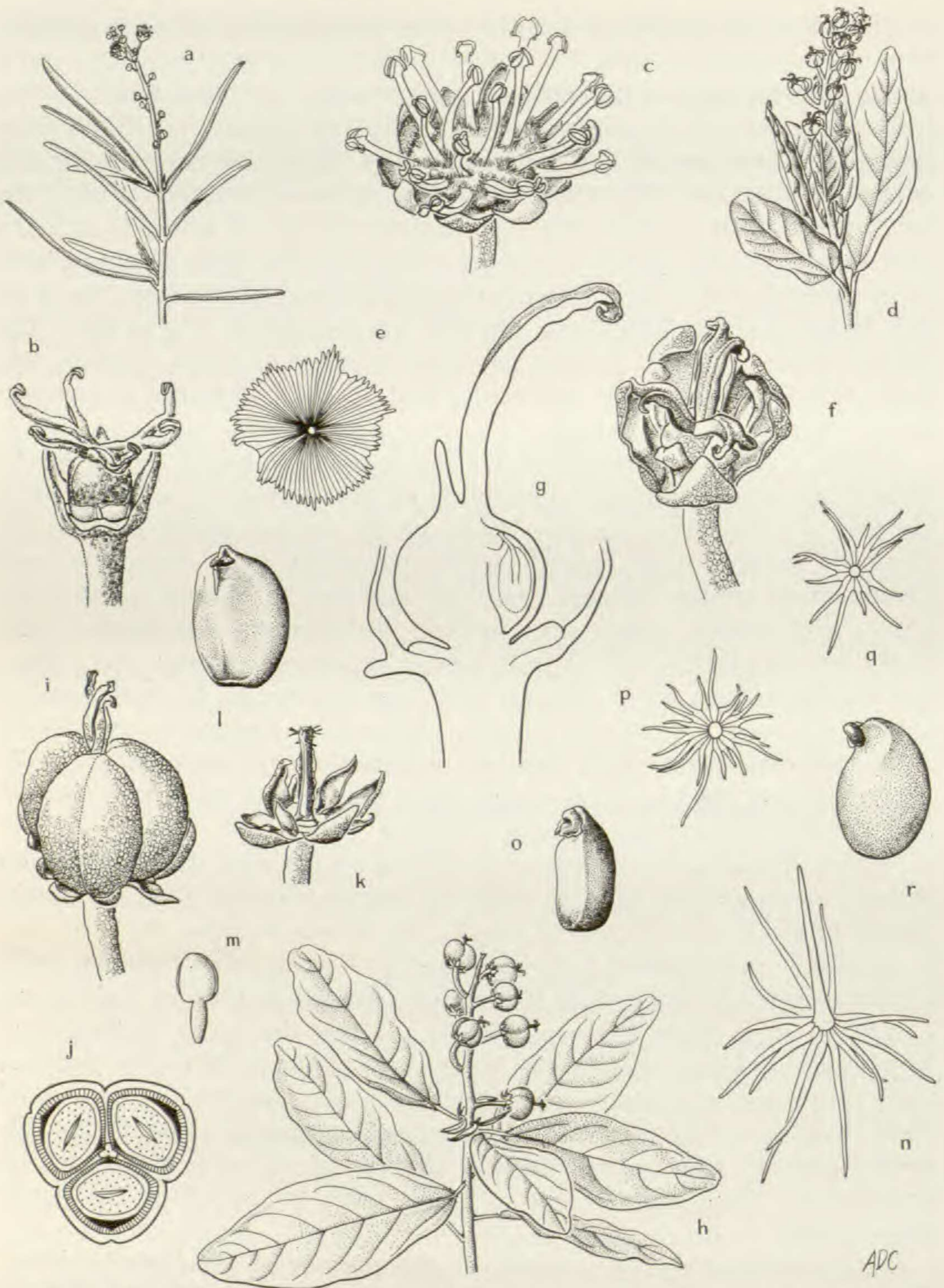


FIG. 2. *Croton*. a-b, *C. linearis*: a, branchlet of male plant,  $\times \frac{1}{2}$ ; b, female flower, two sepals removed to show disc and staminodia,  $\times 6$ . c-m, *C. alabamensis*: c, male flower,  $\times 4$ ; d, flowering branchlet of female plant,  $\times \frac{1}{2}$ ; e, scale from leaf,  $\times 50$ ; f, female flower,  $\times 8$ ; g, same in diagrammatic vertical section to show disc and ovule with nucellus protruding from micropyle into obturator above ovule,  $\times 10$ ; h, branchlet with nearly mature fruit,  $\times 1$ ; i, mature schizocarp before dehiscence,  $\times 2$ ; j, same in diagrammatic cross section to show columella at center, seeds with embryo embedded in endosperm (stippled), and bony endocarps (hatched),  $\times 2$ ; k, persistent sepals, petals, and columella after dehiscence of fruit,  $\times 2$ ; l, seed, adaxial face,  $\times 3$ ; m, embryo,  $\times 3$ .

(Kl.) Muell. Arg., comprising plants with stellate pubescence, is represented in our area by four taxa of controversial relationship. The com-  
 modest and best known, *C. glandulosus* L., occurs from Maryland to Iowa,  
 south to western Texas and Florida, and beyond our limits into South  
 America. It differs from the species so far mentioned in its sharply dentate  
 leaves with large patelliform glands at the base of the blade, male flowers  
 with only seven to nine stamens, and much sparser coat of stellate tri-  
 chomes. In peninsular Florida occur a number of similar populations which  
 have been recognized as separate species. Perhaps the most distinctive is  
*C. arenicola* Small, which includes plants with shorter and much more  
 densely pubescent leaves; it was mistaken for the West Indian *C. betulinus*  
 Vahl by Ferguson. *Croton floridanus* Ferg., on the other hand, is a name  
 applied to plants with much less pubescence than usual. Further studies  
 are needed to determine whether either of these taxa should be ranked as  
 distinct species or whether they should take their place among the plethora  
 of varieties of *C. glandulosus* already recognized by Mueller, Ferguson,  
 and Croizat. A fourth species which seems to be quite distinct, *C. trinitatis*  
 Millsp., is known in our area only from a single collection at Pensacola,  
 but it may be expected in waste places farther south in Florida. It is  
 easily distinguished from *C. glandulosus* by its broader, more coarsely  
 toothed leaves.

A small, entirely North American group of four taxa, sect. HEPTALLON  
 (Raf.) Muell. Arg., well represented in our area, differs little from sect.  
 CROTON except for the calyx of usually six to ten lobes; otherwise, the  
 stellate pubescence and twice bifid styles would relate it to herbaceous taxa  
 of subsect. MEDEA. *Croton capitatus* Michx., as treated by Johnston, is a  
 wide-ranging species with three varieties, two of which, vars. *capitatus* and  
*Lindheimeri* (Engelm. & Gray) Muell. Arg., occur scattered through most  
 of our area, except southern Florida. Further study may show that these  
 "varieties" should indeed be recognized as distinct species. *Croton Elliot-*  
*tii* Chapm., a seldom-collected plant of Georgia and northern Florida, is  
 very similar but has narrower leaves and less deeply divided styles.

Section ANGELANDRA Muell. Arg. includes two annual North American  
 species, both of which occur in our area. Mueller's "key" character of the  
 male calyx "inaequaliter (3-) 5-partitus" was poorly chosen, since the  
 male flowers are in fact not particularly zygomorphic. A more distinctive  
 feature is provided by the rather highly reduced inflorescences often with  
 a single female flower which becomes reflexed (except in an extralimital  
 Texas population). *Croton monanthogynus* Michx., common and wide-  
 spread from Maryland and Iowa, south to Georgia, Texas, and northern  
 Mexico, was made the basis of the genus *Gynamblosis*, primarily because  
 of its female flowers with only two carpels, one of which usually becomes  
 abortive in fruit. However, *C. Lindheimerianus* Scheele, a closely related  
 but coarser and more heavily pubescent species which enters our area in

n, o, *C. glandulosus*: n, hair from leaf,  $\times 50$ ; o, seed, lateral view,  $\times 5$ . p, q,  
*C. punctatus*: hairs from leaf,  $\times 50$ . r, *C. argyranthemus*: seed, lateral view,  
 $\times 5$ .

western Arkansas, has three carpels which develop into a three-seeded fruit; it thus bridges the gap between *C. monanthogynus* and more "typical" taxa of the genus. Johnston has provided detailed descriptions and distribution maps of these taxa as they occur in Texas.

Our last group, sect. DREPADENIUM (Raf.) Muell. Arg., comprises eight or nine American species, mostly of temperate North America (except for the aberrant *C. Eichleri* Muell. Arg. of Brazil). It is set apart from all the other sections by apetalous male flowers and a distinctive pale indumentum of trichomes often more or less intermediate between typical stellate hairs and scales. *Croton punctatus* Jacq. (*C. maritimus* Walt.), the most widespread species, common on sandy coastal beaches from Cape Hatteras, North Carolina, south throughout our area and beyond, differs from related taxa in its long-petioled leaves and monoecious inflorescences. *Croton texensis* (Kl.) Muell. Arg., a dioecious species with narrower, more sparsely pubescent leaves, is adventive in Alabama, according to Johnston. The chromosome number  $2n = 14$ , at variance with all other counts for *Croton*, has been reported from an extralimital species of this section, *C. californicus*; cytological observations on *C. punctatus* would therefore be of especial taxonomic interest.

Recent cytological studies on *Croton* suggest that the genus may prove to have a diversity of karyotype exceeded only by *Euphorbia* (Miller & Webster). Chromosome numbers are now reported from seven sections, and, although scarcely more than ten species have been sampled, it would appear that there are four base numbers represented:  $x = 7$  in sect. DREPADENIUM;  $x = 8$  in sects. ELEUTERIA, GEISELERIA, ANGELANDRA, and CROTON (subsect. MEDEA);  $x = 9$  in sect. ASTRAEA (*C. lobatus*); and  $x = 10$  in sects. CROTON (subsect. CYCLOSTIGMA), ASTRAEA, and HEPTALON. These results suggest that additional chromosome studies, when correlated with anatomical data, will give a considerably better insight into relationships and provide the basis for a much more natural classification.

Froembling, in a rather comprehensive anatomical investigation, showed that there is a tremendous diversity within *Croton*, particularly in trichome conformation and in the distribution of secretory (oil-bearing and laticiferous) elements. Further detailed investigations of trichome types would appear warranted, since it may prove possible to correlate anatomical characters with systematic divisions better than Froembling was able to do. Especially interesting was Froembling's demonstration that many species of *Croton* lack the characteristic "latex"-bearing elements ("Ungegliederte Milchsaftröhren") and that the typical species of sect. ASTRAEA lack oil cells.

Compared with other genera of Crotonaeae such as *Jatropha*, *Hevea*, and *Manihot*, there are few economically important species of *Croton*. The best known, doubtless, is the Asiatic species *C. Tiglium* L., the seeds of which furnish the well-known croton-oil, which possesses properties similar to castor oil or the seeds of *Jatropha Curcas*. At least one American species furnishes a similar substance in the stems which has been utilized under the name of Cascarilla Bark. Unfortunately, the botanical identity of the



plant is uncertain due to long-standing confusion, but it appears probable that it is the West Indian *Croton Eluteria* (L.) Sw. It would not be surprising, however, if further investigation were to show that many other species of *Croton* are also valuable sources of similar substances.

## REFERENCES:

- Under family references see ASSAILLY, BAILLON (1858), BENTHAM, BROWN, CROIZAT (1942; 1945, pp. 188, 189), DEHAY, ERDTMAN, FROEMBLING, GAUCHER, LAKELA & CRAIGHEAD, LANJOUW, LÉONARD, McVAUGH, MARTICORENA, MICHAELIS, MILLER & WEBSTER, MODILEWSKI, MUELLER (1874), NAIR & ABRAHAM, PAX (1884), PERRY, PUNT, RECORD, SMITH, and THATACHAR.
- BACHMAN, O. Untersuchungen über die systematische Bedeutung der Schildhaare. *Flora* 69: 387-400, 403-415, 428-448. *pls.* 7-10. 1886.
- BRACHO, R., & K. J. CROWLEY. The essential oils of some Venezuelan *Croton* species. *Phytochemistry* 5: 921-926. 1966.
- CARABIA, J. P. El género *Croton* en Cuba. *Carib. Forester* 3: 114-135. 1942. [Includes key.]
- . The question of *Croton Eluteria* and *Croton Cascarilla*. *Ibid.* 110-113. 1942. [Reviews problem of botanical identity of the Cascarilla plant; bibliography includes earlier references not included here.]
- CROIZAT, L. New and critical Euphorbiaceae chiefly from the southeastern U. S. *Bull. Torrey Bot. Club* 69: 445-460. 1942. [Discusses spp. delimitation in sect. *Heptallon*.]
- . Preliminari per uno studio del genere *Julocroton* Martius. *Revista Argent. Agron.* 10: 117-145. 1943. [An enumeration, without keys; includes a discussion of reasons for maintaining *Julocroton* as a distinct genus.]
- FARMER, J. An ecological life history of *Croton alabamensis* E. A. Smith ex Chapm. 91 pp. Ph. D. diss. (unpubl.). Univ. Alabama. 1962.
- FERGUSON, A. M. Crotons of the United States. *Missouri Bot. Gard. Rep.* 12: 33-73. *pls.* 4-31. 1901.
- FROEMBLING, W. Anatomisch-systematische Untersuchung von Blatt und Axe der Crotoneen und Euphyllantheen. *Bot. Centralbl.* 65: 129-139, 177-192, 241-249, 289-297, 321-329, 369-378, 403-411, 433-442. *pls.* 1, 2. 1896.
- GEISELER, E. F. *Crotonis monographiam.* x + 83 pp. Halle. 1807.
- HOOKE, J. D. *Croton Eluteria*. *Bot. Mag.* 123: *pl.* 7515. 1897. [Construes the Cascarilla bark species in the same sense as Carabia.]
- JOHNSTON, M. C. The Texas species of *Croton*. *Southwest. Nat.* 3: 175-203. 1959.
- & B. H. WARNOCK. The ten species of *Croton* (Euphorbiaceae) occurring in far western Texas. *Southwest. Nat.* 7: 1-22. 1962. [Includes descriptions of some spp. found in the southeastern U. S.]
- LÉONARD, J. Observations sur les plantules de quelques *Croton* du Congo. *Bull. Soc. Bot. Belg.* 94: 23-28. 1962. [Notes on some systematic implications of seedling morphology.]
- MARCHAND, L. *Du Croton Tiglium.* Recherches botaniques et thérapeutiques. 94 pp. 2 *pls.* Paris. 1861. [Includes excellent illustrations of habit and floral details; botanical part also printed in *Adansonia* 1: 232-245. 1861.]
- MOHR, C. The last addition to the shrubs of eastern North America (*Croton alabamensis*). *Garden Forest* 2: 592, 594. 1889. [Illustration inaccurate in some respects.]

SZWEYKOWSKI, J. Translocation heterozygosity in *Croton californicus*. *Madroño* 18: 31. 1965.

TAILLANDIER, M. Étude biochimique du latex de *Croton gossypifolius*. 120 pp. Lons-le-Saunier. 1939.\*

10. *Crotonopsis* Michaux, Fl. Bor.-Am. 2: 185. *pl.* 46. 1803.

Delicate annual herbs, stems and foliage with lepidote trichomes; latex absent. Leaves alternate, or subwhorled below branching-points; stipules obsolete; petioles short; blades entire and without basal glands. Plants monoecious; flowers in abbreviated spiciform racemes, bracts 1-flowered. Flowers with pentamerous calyces; calyx lobes imbricate. Male flowers: petals present, imbricate; disc dissected into 5 small segments; stamens 5, opposite the petals, free, filaments incurved in bud; pollen globose, inaperturate, clavate; gynoecium vestigial or absent. Female flower: calyx lobes 3–5, more or less unequal and some lobes often obsolete; disc inconspicuous, deeply lobed or divided; petals absent; carpel solitary; style twice or more bifid; ovary lepidote; ovule solitary, anatropous. Fruit dry, achene-like, indehiscent; seed solitary, not carunculate; seed coat smooth and thicker than carpel wall; endosperm copious; embryo straight, cotyledons broader than and about as long as the radicle. TYPE SPECIES: *C. linearis* Michx. (Name alluding to resemblance of the plant to herbaceous species of *Croton*.)

A genus of two species confined to eastern temperate North America. In branching pattern, leaves, and the characteristically reduced inflorescences, these plants somewhat resemble herbaceous species of *Croton*, especially *C. monanthogynus* Michx., of sect. ANGELANDRA. However, the indehiscent unicarpellate fruit with an ecarunculate seed is quite different from the dehiscent fruit with carunculate seeds of *C. monanthogynus*. While it would scarcely do any violence to nature to combine *Crotonopsis* with *Croton*, the group is sufficiently distinctive and well characterized to make it seem best to let it stand as an independent genus.

Although Gray and Chapman, as well as many other floristic writers, followed Pursh in construing the genus as containing but a single species, Pennell showed that there are two and gave a clear summary of their distinctions. *Crotonopsis linearis* Michx., recognizable by its narrow leaves with equal-rayed stellate hairs above, elongated 3–6-fruited spikes, and fruits with small pale scales, occurs from South Carolina, south to Florida, and west to Missouri and Texas, with a disjunct population in eastern Iowa and northwestern Illinois. *Crotonopsis elliptica* Willd., often confused with *C. linearis*, may ordinarily be distinguished by its relatively broad leaves which are more densely and coarsely hispid-stellate above (due to unequal development of one of the radii of the hairs); more abbreviated spikes with only one or two female flowers; and fruits with darker and larger scales. Furthermore, in *C. elliptica*, branching occurs closer to the base so that the plants often are lower and more spreading than the erect, more sparsely branching plants of *C. linearis*. *Crotonopsis*

*elliptica* has a much broader range than its sister species, as it is known to extend from New Jersey south to northern Florida, and west to Texas, southeastern Kansas, and southern Illinois. According to reports in the literature (e.g., McVaugh; and on specimen labels) it is a characteristic species of bare sandstone or granitic outcrops, although it may occur in disturbed weedy habitats as well. In contrast, *C. linearis* is most often found in sandy soil in clearings or open woods.

## REFERENCES:

Under family references see FROEMBLING, MICHAELIS. Under *Croton* see BACHMAN.

McVAUGH, R. The vegetation of the granitic flat-rocks of the southeastern United States. Ecol. Monogr. 13: 120-166. 1943. [Includes distribution map of *C. elliptica*.]

PENNELL, F. Notes on plants of the southern United States — IV. The genus *Crotonopsis*. Bull. Torrey Bot. Club 45: 477-480. 1918.

(To be concluded)